

FLORAL STRUCTURE, COLORATION, AND EVOLUTION
OF BIRD-POLLINATED PLANTS; CORRELATION WITH
FUNCTIONAL TRAITS IN NECTARIVOROUS BIRDS

INAUGURAL-DISSERTATION
zur Erlangung der philosophischen Doktorwürde
vorgelegt der
Philosophischen Fakultät II
der Universität Zürich

von
ROLF BAUMBERGER
von Neuenburg und Koppigen/BE

Begutachtet von den Herren
Prof. Dr. C.U. Kramer
Prof. Dr. R. Wehner

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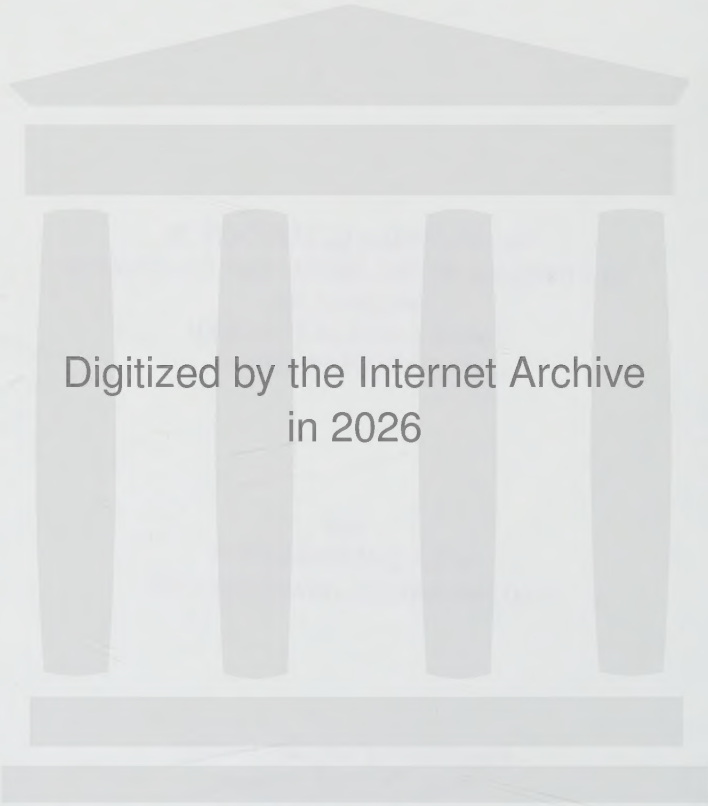
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1. INTRODUCTION

Flowering plants usually have their flowers adapted to take maximal advantage of one or more classes of pollinatory agents, whether these be physical or biotic. Floral morphology and behaviour have evolved conjointly, combining to maximize pollinator attraction, to increase the likelihood of suitable fertilization, and to discourage visits by ineffective pollinators.

Particular combinations of floral morphology and behaviour, often referred to as syndromes, have been reported as typifying plants serviced by different pollinator groups (Faegri & van der Pijl 1966; Baker & Hurd 1968; Percival 1965; Proctor & Yeo 1973). According to these authors eight or more different syndromes of biotic pollination are known, including five syndromes of invertebrate pollination (beetle, fly, bee, butterfly, and moth), and four syndromes of vertebrate pollination (birds, bats, marsupials, and rodents).

The present thesis re-examines the syndrome of ornithophily, the pollination of flowers by birds. Although this syndrome has been summarized in Faegri & van der Pijl (1971), a statistical description of structural regularities such as colour and shape as functional features of bird flowers is here presented anew.

The question is, whether or not one can put forward a generalised, hypothetical, hierarchically-structured model that will integrate the functional features, ecology and evolution of bird-pollinated flowers all over the world. A possible model concerning the coloration and shape of bird flowers is presented in section 4.3.

Waser (1983) maintains that flower colours have somehow evolved to maximize their coverage of the pollinator visual spectra, and to minimize competition between bird-pollinated plant species when their density is high. The present work will concentrate on showing whether or not there is such a correlation between the density of bird flower species and the degree of spectral coverage of their flower colours. In addition, it will address the questions as to whether bird flowers can be classified according to their colour patterns; whether these hue-distinct flower classes can be interpreted ecologically and/or evolutionarily; and finally whether similar classes occur only locally or are also to be found worldwide.

The classification of colours also includes the reflection of flowers in near UV-light (310-390 nm wavelength), thus serving to clarify whether or not UV-patterns on bird

flowers are frequent.

A further question is whether, and to what extent, bird-pollinated flowers possess colour patterns which may act as nectar-guides. Nectar-guides are contrastingly pigmented parts of flowers which serve as advertiser for animals where nectar is to be found. The entrances to corollas, corolla limbs, anthers, styles, and pollen are frequently of contrasting colours. Such patterns may act as targets for flower-birds (Waser, 1983). Are they the rule or merely an exception?

Flowers pollinated by large animals such as bats, birds, or hawkmoths produce relatively large volumes of nectar compared to flowers pollinated by small animals like butterflies and small moths (Cruden et al., 1983). A general question arises as to whether there is a correlation between tube-length, or spur-length, and the amount of nectar in bird-pollinated plants. Berry (1982) stated that, in Ecuador, in the bird-pollinated section of *Fuchsia*, two closely related species differing mainly in floral tube-length and coloration, nevertheless occur together or in close proximity without the presence of intermediate plants. This patterns suggests, according to Berry, that hummingbird species are species-specific pollinators of *Fuchsia*, the specificity being linked to tube-length and colour patterns, or that flower dimensions act mechanically against interspecific pollination. This idea of a correlation between floral tube-length and coloration and/or quantity of nectar will be developed in the following pages.

Flowers of a given syndrome often lack one or more of the expected features. Californian bird flowers may have evolved from insect-pollinated ancestors (Grant & Grant, 1968). I would suspect that these bird-pollinated plants may still carry features of insect-pollinated plants, such as UV nectar-guides, hairy ridges or smell.

Finally I examine the degree of coevolution between birds and plants. More precisely, I attempt an assessment of which features may have been particularly involved in such coordinated patterns of mutual adaptation as coevolution implies.

1.1 Materials and Methods

a) Colour Separation Photography

Colour separation photography of the flower, in the red, orange, green, blue, violet and ultraviolet part of the spectrum was achieved with an Edixa-Iscotar lens (1:2,8/50) equipped with corresponding filters. Kodak Wratten filters were used; number 25 for red, 22 for orange, 58 for green, 47B for blue, 35 for violet, and 18A for ultraviolet (UV) separation. The lens plus UV filter has a cut-off at 310 nm wavelength. Kodak Tri-X black-and-white film was used. For measuring colour reflectance a grey scale was produced according to the method of Kevan et al. (1973).

b) Colour Identification

For colour identification of living plants the Methuen Handbook of Colour was referred to. Its thirty A8 samples are specified in the CIE chromaticity diagram (Fig. 1). The colour dictionary of this book was cross-referenced when classifying colour names from literature.

Fig. 1

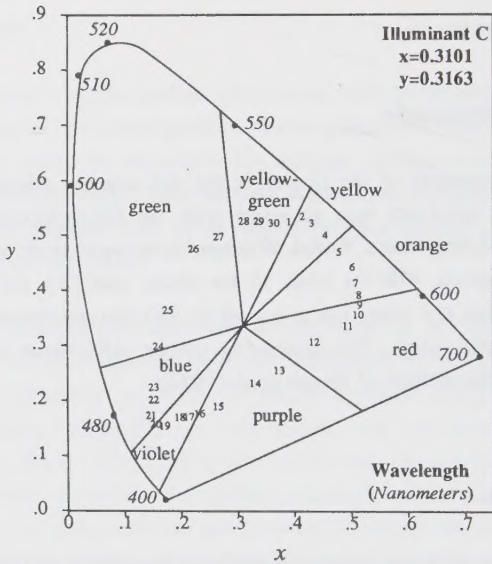


Fig. 2

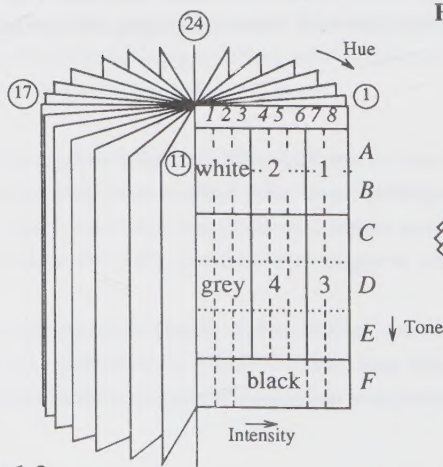
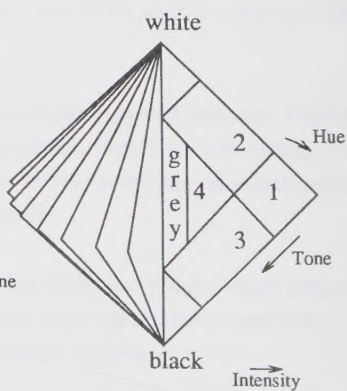


Fig. 3



Figures 1-3

1. CIE Colour specifications of the A8 samples 1-30 (Methuen Handbook of Colour) and areas with unitary hue names.
2. Cylindrical colour space of Methuen Handbook of Colour with classified areas 1-4 as well as white grey and black.
3. The same, but transformed into a double-coned space.

For statistical purposes the following plates were unified by unitary hue names:

Plate 28-30 and 1	as Yellowish Green
Plate 2- 4	as Yellow
Plate 5- 8	as Orange
Plate 9-12	as Red
Plate 13-16	as Purple
Plate 17-19	as Violet
Plate 20-23	as Blue
Plate 24-27	as Green

When the intensity was less than '4' and tone less than 'C', the colour was classified as white. When the tone was darker than 'E' the colour was named 'black' (Fig. 2 and 3).

Together with the flower, the coloured bracts, spathes, and other coloured parts of the plant were considered as a unit of attraction. The whole surface of this unit was taken to be 100 percent. If multicoloured, this unit was split into subsurfaces, and their various percentages were estimated.

c) Corolla length, Bill length, Amount of Nectar

Corolla lengths of living plants in California and of herbarium specimens (of herbaria of Zurich, Geneva, the Rancho Santa Ana Botanic Garden, Claremont, California, and of the Bishop Museum, Honolulu, Hawaii) were measured by introducing scaled (mm) pipettes into the corolla tube. The distance from the nectar sphere to the edge of the tube in millimeters was taken to be the effective corolla length.

Nectar quantity of 37 Californian plants was also measured with micropipettes and expressed in microliters (μ l). Over 120 bills of flower-birds from the Zoological Museum of the University of Zurich were measured for statistical purposes. If the bill was decurved, the chord length was taken.

d) Study sites, other sources

An array of living Californian wild plants was analysed according to the methods already described under b & c during the author's field work from April to September 1983. For identifying the specimens, the following literature was used by way of comparison: Munz (1973), Jaeger (1979), Powell & Hogue (1979), and Carlquist (1980). Further data (nectar quantity, flower-shape, -dimension, -coloration, and kind of pollinator) from ornithophilous plants for statistical purposes were found in:

Ali, (1931); Amadon, (1950); Armstrong, (1979); Atsatt & Rundel, (1982); Baker & Baker (1983); Baumberger (1982); Berry, (1982, 1985); Bertin, (1982); Bishop & Herbst, (1973); Breedlove, Berry & Raven, (1982); Brown & Kodric-Brown, (1979); Cammerloher, (1928); Carlquist, (1980); Carpenter, (1976, 1978, 1979); Corbet & Willmer, (1981); Cowling & Mitchell, (1981); Crosswhite & Crosswhite, (1981); Cruden, (1972); Cruden & Toledo, (1977); Dahlgren et al., (1979); Docters van Leeuwen, (1932); Eyde & Morgan, (1973); Feehan, (1985); Feinsinger et al., (1978, 1979, 1982); Finsch, (1965); Ford, (1985); Ford et al., (1979); Freeman & Worthington, (1985); Frost & Frost, (1980, 1981); Gill & Wolf, (1975); Grant & Grant, (1965, 1968, 1981); Guillardmod et al., (1979); Hall & Moreau, (1979), Harteret, (1900); Henrickson, (1972); Hernandez & Toledo, (1979, 1982); Hodgson & Paine (1971); Howard & Moore, (1980); Iwarsson, (1979); Jeppesen, (1981); Keighery, (1982); Krukoff, (1938, 1982); Krukoff & Barneby, (1974); Lack, (1973); Leck, (1974); Linhart, (1973); Luther, (1972); Maas, (1972); MacDonald, (1973); McDade & Kinsman, (1980); Morony et al., (1975); Morton, (1979); Opler, (1983); Paige & Whitham, (1985); Percival, (1965); Pijl, (1937); Plitmann, Raven & Breedlove, (1973); Proctor & Yeo, (1973); Raven, (1974, 1976); Ridgway, (1911); Rieper, (1980); Rock, (1919, 1957, 1962, 1974); Roubik, (1982); Roubik, Holbrook & German, (1985); Rust, (1977); Schuchmann, (1979); Scogin & Freeman, (1984); Scott et al., (1982); Siegfried, (1983); Singh, (1929); Skead, (1967); Smith & Downs, (1974); Snow & Snow, (1972); Spira, (1980); Steiner, (1979); Stiles, (1973, 1975, 1976); St. John, (1939, 1973, 1975, 1981); St. John & Hosaka, (1935, 1938); Sytsma & Pippen, (1985); Toledo, (1974); Toledo & Hernandez, (1979); Tomlinson et al., (1978, 1979); Vissre, (1981); Vogel, (1954, 1980); Vogel et al., (1984); Wagner, (1946); Waser, (1978, 1979, 1983); Werth, (1915); Wiens & Toelken, (1979); Wimmer, (1943, 1953).

e) Data base, computer programs

Data (details are already given under b, c, and d) from flowers and birds were written into a data file and were analysed with the help of some computer sorting-programs and the statistics of SAS.

The following tables and figures are based on these investigations:

Tables 3, 4-6, 8.

Figures 4, 8-13, 16-35.

2. VISUAL SPECTRA OF NECTAR-BIRDS AND REFLECTANCE SPECTRA OF BIRD FLOWERS

2.1 Colour vision and visual spectra of nectarivorous birds

For animals a spectral range from 300 nm to 800 nm is available for vision, this being the limited range of the electromagnetic radiation spectrum reaching the Earth's surface which can cause photochemical reactions. However, the actual limits of animal vision are determined by the visual pigments contained within the photopic receptors of the retina, the cones, and by pre-receptor filters (Bowmaker, 1980). In man, these are principally the lens that cuts off light below about 400 nm, and the macula pigment in the yellow spot on the retina. The second limit, at about 700 nm in the red, is determined by the limited sensitivity of the red cones.

Nectarivorous birds also have colour vision, as has been clearly demonstrated for hummingbirds (Poley, 1968; Goldsmith et al., 1979) and sunbirds (Doerr, 1979).

According to Goldsmith et al. (1984) hummingbirds' retinas have five classes of oil droplets, four of which have the properties of sharp-cut longpass filters in the visible range of the spectrum. These droplets are not likely to be the basis of UV vision. A fifth transparent droplet, together with some cones maximally sensitive at 370 nm, may act as an UV receptor (Chen et al., 1984). In hummingbirds the authors suggest a visual border at 340 nm in the near UV. This spectral sensitivity of the UV-sensitive cone was measured extracellularly in opened eyecups. As shown by experiments based on trained visual discrimination, however, hummingbirds are not able to differentiate between filters transmitting light of 370 nm wavelength and non-transmitting filters (Huth & Burkhardt, 1972). The characteristics of the oil droplets may vary interspecifically in hummingbirds (Goldsmith, 1984).



2.2 Reflectance spectra of hummingbird-pollinated flowers

To have at one's disposal data comparable to those for birds' visual spectra, spectral reflectance curves from an array of hummingbird flowers should be available. This is not the case. The missing spectral reflectance was approximately estimated by the following procedure. First, for each of the saturated colour patches of the Handbook of Colour the reflectance (in the red, orange, green blue, and violet) was determined photographically. These reflectance values were then cross-referenced with the tables of the colour statistics of flowers based on this Handbook.

As a result a frequency distribution of the dominant reflecting wavelengths for 684 hummingbird flowers was obtained (Fig. 4). From this it can be seen that the dominant wavelengths of reflecting floral parts are concentrated in the green-red segment of the spectrum.

But this method yields no information about the reflectance in the UV. For this purpose I determined the reflectance of 38 Californian bird-pollinated flowers. The reflectance was weak (up to 12%) in the near UV (310-395 nm), contrary to that of bee flowers (Table.1).

Similar results were obtained by Kugler (1970), Baumberger (1982), Straw (1956), and Olesen (1985), whereas Burkhardt (1982) found three out of four bird flowers to have UV-reflecting corollas. A further unpublished study on this subject in the Caribbean, however, failed to show UV-patterns on floral parts (Burkhardt, personal communication). Only white hairs and small, brightly coloured parts of flowers may reflect UV to any significant degree.

To conclude, the frequency of the dominant wavelengths of reflected light in bird flowers is high in the red and gradually declines towards the near UV end of the spectrum. UV patterns and strong UV reflections of floral parts, as frequently observed on bee flowers (Kugler, 1970), are not common in bird flowers. This implies that potential nectar-guides on bird flowers are probably situated within the human visual range.

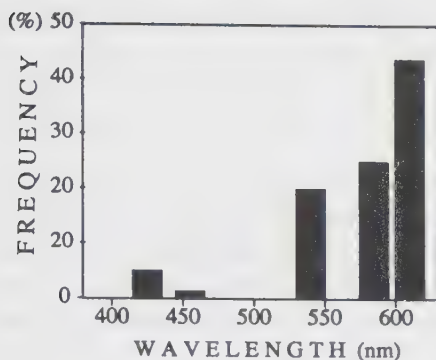


Fig. 4

Relative frequency distribution for dominant wavelengths of 684 hummingbird flowers.
(Source material see section 1.1 e).

Table 1 UV reflectance (in %) of Californian bird-pollinated flowers
(author's field observations)

<i>Aquilegia formosa</i>	6 - 10	<i>Lilium maritimum</i>	5
<i>Brodiaea ida-maia</i>	5	<i>L. parvum</i>	5
<i>Castilleja affinis</i>	5 - 9	<i>Lobelia cardinalis</i>	5 - 9
<i>C. angustifolia</i>	8 - 17	<i>Nicotiana glauca</i>	5 - 11
<i>C. applegatei</i>	5 - 7	<i>Mimulus aurantiacus</i>	5 - 9
<i>C. breweri</i>	6	<i>M. cardinalis</i>	5
<i>C. chromosa</i>	5 - 6	<i>M. parviflorus</i>	8
<i>C. foliolosa</i>	5 - 8	<i>Penstemon bridgesii</i>	5 - (60) ^a
<i>C. latifolia</i>	6 - 13	<i>P. centranthifolius</i>	7 - 10
<i>C. miniata</i>	5 - 7	<i>P. clevelandii</i>	8
<i>C. franciscana</i>	6	<i>P. eatonii</i>	5
<i>Delphinium nudicaule</i>	9	<i>P. labrosus</i>	5 - (40) ^a
<i>Dudleya sp.</i>	5	<i>P. newberryi</i>	6 - 11
<i>Galvezia speciosa</i>	6	<i>Sarcodes sanguinea</i>	5 - 7
<i>Echinocereus mojavensis</i>	6 - 9	<i>Salvia spathacea</i>	5 - 12
<i>Epilobium sp.</i>	5 - 12	<i>Silene laciniata</i>	6
<i>Ipomopsis aggregata</i>	5 - 10	<i>Stachys chamissonis</i>	6 - 30
<i>Keckiella cordifolia</i>	6 - 10	<i>Trichostema lanatum</i>	8
<i>K. ternata</i>	5 - 11		

^a Reflectance of white hairs

3. CLASSIFICATION OF BIRD FLOWERS AND NECTARIVOROUS BIRDS

3.1 Classification of bird flowers

3.1.1 Shape The observation that pollination units from different taxa and of different morphological value are pollinated in the same way, naturally led to attempts to classify flowers according to their functional structure (Faegri & Pijl, 1971). These workers have summarized the blossom preferences of the main groups of pollinators. According to them blossoms are dishbowl-, bellbeaker-, brush-, gullet-, flag-, or tube-shaped.

A bird-pollinated flower may be flag-shaped as instanced in *Erythrina indica* floral structure, bell-shaped (*Canarina canariensis*), gullet-shaped (*Salvia spathacea*), brush-shaped (*Eucalyptus spp.*), or most frequently, tube-shaped. A much more sophisticated pollination syndrome is found in the hemiparasitic tropical mistletoes (Loranthaceae). In some genera an explosive flower-opening mechanism has been described (Wiens & Toelken 1979, and Feehan 1985).

There are differential characteristics between flowers for hummingbirds (hovering birds) and flowers for perching birds. Hummingbird flowers stand out or hang down towards the free space, readily accessible to pollinating hummingbirds. Hummingbird flowers are predominantly tubular, the tube often being straight and varying from 3.5 mm up to 130 mm in length, depending on the plant species. This coincides with the structure of hummingbird bills which is thin, long, and almost straight or moderately decurved. The straight floral tubes of hummingbird flowers are needed by their pollinators, which are only capable of feeble forward motion while hovering.

But decurved floral tubes do occur in *Heliconia* species of the South American tropics (Stiles, 1975). In this region, however, there lives the only hummingbird with a very strongly decurved bill, namely *Eutoxeres aquila*, which uses a perching mode of exploiting flowers. This bird exclusively visits the strongly decurved flowers of *Heliconia pogonantha* in Finca La Selva (Stiles, 1975).

In the remaining flowers of the New and Old World, Australia, and the Hawaiian Archipelago, either there is a perch near the flowers and the flowers point toward it (Faegri & van der Pijl, 1971), or, as is the case in Australia, the flowers of a number of plant species are pollinated by birds standing on the ground (Keighery, 1982).

When the flowers are both tubular and long, they are moderately to strongly curved and well suited to their pollinator's bill. Obviously a perching bird can more easily get access to the flowers if it has a curved bill rather than a long straight bill, since it can then simply incline its head downwards when probing the flowers.

In both the Old and New World an array of open-mouthed flowers exists, like *Spathodea campanulata*, *Puya* and *Erythrina fusca* flowers, for which passerine pollination is documented (Steiner, 1979; Morton, 1979; Toledo & Hernandez, 1979; Ali, 1931; Docters van Leeuwen 1932; Porsch, 1924; Singh, 1929). In these cases, the pollinating birds have a relatively unspecialized and shorter bill.

In section 4 I shall try to supply an answer to the question as to why floral-tube length and bill length may sometimes be extremely large.

3.1.2 Rewards

Flowering plants that are pollinated by birds produce nectar in their flowers as the sole reward for potential pollinators. The nectar consists of water, sugar (sucrose, fructose and glucose), and of amino acids. There is a general relationship between nectar sugar concentration, the respective proportions of the constituent sugars, and pollinator type (Baker & Baker, 1983; Table 2).

Hummingbird and sunbird-pollinated flowers generally have medium rates of nectar secretion, medium sugar concentration, and their nectar is sucrose-rich with only traces of amino acids. Passerine or "perching" bird flowers, on the contrary, secrete large quantities of dilute nectar whose composition is poor in sugar (mainly sucrose), while the concentration of amino acids is almost always high (Steiner, 1979; Cruden & Toledo, 1977; Toledo & Hernandez, 1979).

I could not discover any significant relationship (with SAS regression procedures) between effective corolla length and the amount of nectar secretion in 60 investigated taxa of hummingbird flowers ($r = .023$).

3.1.3 Basic Colours

Flowers are coloured to maximize attractiveness for visitors. Bird flowers are often multi-coloured, so that we shall differentiate between basic colours and secondary or complementary colours. The basic colour is that with the highest surface area and covers 51-100% of the total unit of attraction. By definition, the surface of secondary colour tissue does not exceed 49 percent of the unit of attraction.

The unit of attraction consists of the flower(s), the bracts, and other coloured plant parts adjacent to the flower. The basic colour of bird flowers is enhanced by secondary colours in half the investigated taxa.

Table 2 Nectar volume, nectar concentration, and sucrose:hexose ratio per flower of the named flower classes.

Pollinator	Range ^a µl Nectar	Range ^a sugar conc	S/G+F ^b	Amino Acids ^b
Bat	65 - 182 (123)	13-27 (20)	< .5	weak
Hawkmoth	3.4 - 84 (43)	14-29 (26)	> .5	low
Hummingbird	1.2 - 110 ^c (--)	9-35 (22)	> .5	weak
Sunbird	6 - 57 (32)	15-22 (18)	< .5	weak
Honeyeater	- - -	- - -	< .5	weak
Honeycreeper	- - -	- - -	< .5	weak
Oriol-Starling	48 - 650 (350)	5-10 (7.5)	< .1	rich
Bee	.14 - 7.4 (3.7)	20-45 (32)	.1-1	modest
Butterfly	.58 - 4.0 (2.25)	5-50 (27)	.1-1	high

a) Cruden et al. (1983)

b) Baker & Baker (1983) S: sucrose, G: glucose, F: fructose

c) this study

The figures in brackets indicate the average measures for each category sampled.

Table 3 gives the basic floral colours (petals, stamens or bracts) of four regions of the world where bird flowers are common. While it is true that the predominant colour of bird flowers is red (the world average is 47%), non-red flowers constitute an equally important colour group, at least for ornithophilous plants occurring outside the Hawaiian

Archipelago. In these islands red flowers are not well represented in terms of numbers (25 species or subspecies); but even there, the few red-flowered *Metrosideros*, richly flowering trees with brush-shaped flowers, predominate by sheer abundance over non-red flowers. These trees are by far the most abundant nectar resource for the endemic Drepanid birds on these islands (Carpenter, 1976).

Over 90% of bird flowers in the world are brightly coloured, i.e., red, white, orange, yellow-green, or yellow. The least common colours are black, blue, brown, purple, and violet, and all these together account for the remaining 9.9%. These dull-coloured and inconspicuous flowers have been documented in Eastern Australian Rutaceae of the genus *Adenanthos* (Armstrong, 1979), in the Leguminosa *Kennedia* (Keighery, 1982), in the Hawaiian Lobelioids of the genera *Clermontia*, *Cyanea*, *Lobelia*, *Trematolobelia*, and *Rollandia*, and also in *Hibiscus* of the Malvaceae (Rock, 1919; Carlquist, 1980), in the New World Geraniaceae with *Geranium*, North American Scrophulariaceae including the genera *Castilleja* and *Penstemon* (Grant & Grant, 1968), and finally in the Campanulaceae as evidenced by *Burmeistera* and *Centropogon* in the South American tropics (Jepesen, 1981).

Another unusual aspect of flower colour is that the flowers in Australia and the Hawaiian Archipelago are more often yellow and white than the flowers in the rest of the world. This is probably due to the absence of appropriate insect pollinators and the consequent relative scarcity of yellow and white entomophilous plants, leaving these colours to be taken over by bird flowers in these regions of the world (Ford et al., 1979, Carlquist, 1980).

The common bee flower colour violet is very rarely found as primary colour in bird flowers throughout the world.

3.1.4 Secondary Colours

Secondary colours or complementary colours are often present on bird flowers. Colour patterns formed by such complementary colours were found on 584 out of 1117 flowers recorded (52%). Here it should be noted that the data collected are partially incomplete with respect to the frequency of occurrence of secondary colours so that their actual abundance might be higher in reality. Although there can be up to three secondary colours in a unit, one contrasting colour is the rule (72%), two and three secondary colours being relatively exceptional (25% and 3%, respectively).

The contrastingly coloured area is often sharply bordered, or restricted to particular floral parts. These include corolla limbs, corolla lobes, sepals, petals, anthers, stigmas, or even whole flowers when bracts or spathes are also coloured (as seen in *Castilleja* and *Bromeliaceae*). Sometimes floral parts are spotted, as in *Anigozanthos*, and also at the entrance to the nectar in *Clianthus*. Stripes or lines are found in *Malvaceae* species and in Hawaiian Lobelioids of bird-pollinated plants.

These contrasting-coloured areas are not randomly arranged. On the contrary, the contrastingly pigmented tissues are found, at least in red-coloured flowers, around the entrance to the corolla, as if advertising where nectar is to be found (Werth, 1915; Toledo & Hernandez, 1979). Although birds are adept at finding an entrance, such patterns may enable birds to reduce the handling time within and between flowers (see Waser, 1983).

Table 3. Number (N) and percentage of bird flower colours of the world

Colour	World		Australia ^a		Hawaii		New World		Old World	
	N	%	N	%	N	%	N	%	N	%
Red	780	47.1	274	45.1	25	11.4	383	60.1	98	50.5
White	281	17.0	148	24.3	87	40.0	34	5.3	12	6.1
Orange	189	11.4	25	4.1	4	1.8	102	16.0	58	29.7
Yellow	162	9.8	132	21.7	3	1.4	23	3.6	4	2.0
Purple	92	5.5	3	0.5	38	17.4	48	7.6	4	2.0
Y.-Green	80	4.8	15	2.5	13	6.0	36	5.6	16	8.2
Black	32	1.9	2	0.3	28	12.8	1	.1	1	.5
Grey/Brown	17	1.0	9	1.5	6	2.7	-	-	-	-
Blue	12	.7	-	-	11	5.0	1	.1	1	.5
Green	11	.7	-	-	3	1.4	8	1.3	1	.5
Violet	2	.1	-	-	-	-	2	.3	-	-

a) Data from Keighery (1982)

Such patterns are illustrated in Fig. 5-7. It is noteworthy that the nectar-guide colour may dominate the basic colour in frontal view (Fig. 5-6), which is precisely the birds' view when hovering in front of the flower.

In *Lobelia laxiflora* a colour change in the nectar-guide also occurs (Fig. 7). During anthesis, a number of flowers in different stages of anthesis hang on the same plant. The old but not yet faded flowers still attract potential pollinators to the plant, but are less attractive in close-up because their nectar-guides have lost most of their contrastive coloration.

Secondary colours on bird flowers are ubiquitous. As is the case with the basic colours, most (80%) belong to the bright colours, viz. yellow, yellow-green, white, red, and green. Especially notable are the numerous yellow patterns, particularly on red flowers (33.5%, Table 4).

Frequent primary colours are red and orange, frequent secondary colours are yellow (less so in Australia) and violet. Colours which can be found both in primary and in secondary rôles are yellow-green, white, purple, green, black, and blue.

On red flowers, yellow, black, white, yellow-green, and violet patterns are frequent, whereas orange, purple, green, and blue are not (Table 5.). 19 % of red flowers have more than one additional colour. When the first additional colour is not a frequently occurring one, the second and third are infrequent too, and conversely. Thus, red flowers with a common yellow nectar-guide most often have additional secondary colours.

Flowers with orange basic colours have almost the same additional secondary colours as red flowers do, with the exception of violet, which is practically absent.

Yellow and yellow-green flowers have a whole range of secondary colours, such as white, purple, black, red, orange, and violet.

Black and white contrast is found on white and black flowers. White flowers have yellow-green, red, purple, and black marks on their corollas. Similarly, purple and black flowers have light colours, such as yellow-green and white, as secondary colours.

Fig. 5

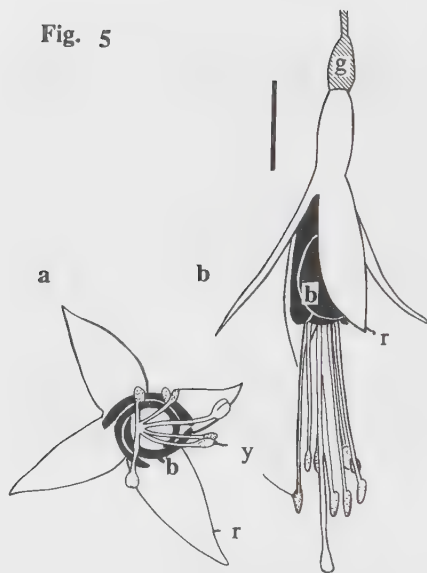


Fig. 6

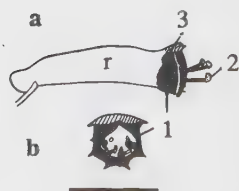
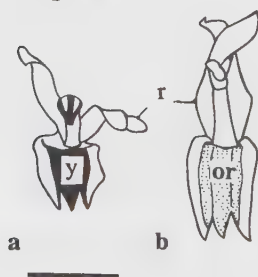


Fig. 7



Figures 5-7

Contrasting colour patterns on red flowers serving as nectar-guides.

5a-b. *Fuchsia magellanica*. a) lateral view, b) frontal view; b = bluish-violet, g = green, r = bluish-red, y = yellow.

6. *Cuphea ignea*. a) lateral view, b) frontal view; r = red, 1 = purplish-black, 2 = yellow, 3 = white.

7. *Lobelia laxiflora*. Colour change of nectar-guide in late anthesis. a) early, b) late anthesis; r = red, y = yellow, or = orange.

Bars indicate 1 cm. Drawings based on living plant materials cultivated at the Botanical Garden of Zurich, Switzerland.

Table 4

Number (N) and percentage of bird flower secondary colours

Basic Flower Colour	SECONDARY COLOURS									
	Yellow	Y.-Gr.	White	Purple	Black	Red	Orange	Violet	Green	Blue
Red	191	66	68	8	18	-	20	24	5	-
White	4	7	-	28	8	7	3	-	1	2
Orange	27	26	12	8	7	18	-	1	1	-
Yellow	-	5	1	2	-	6	2	-	-	1
Purple	4	11	12	-	7	2	1	2	1	-
Y.-Green	3	-	8	8	4	6	6	4	-	1
Black	-	2	5	4	-	1	-	-	-	-
Blue	-	3	-	-	-	-	-	-	-	-
Green	-	1	2	4	1	-	1	1	-	-
Violet	-	-	1	-	-	-	-	-	-	-
N	229	121	109	62	45	40	33	32	8	4
in %	33.5	17.6	16.0	9.1	6.6	5.9	4.8	4.7	1.2	0.6

Table 5

Distribution of secondary colours on red flowers

SECONDARY COLOURS															
First		Second								Third					
N	Colour	N	yg	wh	ye	or	vi	bl	pu	N	or	ye	bl	vi	pu
173	Yellow	32	9	12	-	2	5	1	2	4	-	1	2	-	1
63	White	13	5	-	4	2	1	1	-	3	2	-	-	1	-
48	Y.-Green	14	1	3	3	4	1	1	1	1	1	-	-	-	-
19	Violet	4	-	1	3	-	-	-	-	0	-	-	-	-	-
17	Black	2	1	-	1	-	-	-	-	0	-	-	-	-	-
6	Orange	3	1	2	-	-	-	-	-	0	-	-	-	-	-
5	Purple	1	1	-	-	-	-	-	-	1	-	1	-	-	-
4	Green	4	-	-	4	-	-	-	-	1	-	-	-	1	-
0	Blue	0	-	-	-	-	-	-	-	0	-	-	-	-	-
334		73	18	18	15	8	7	3	3	10	3	2	2	2	1

yg = yellow-green, wh = white, ye = yellow, or = orange, vi = violet, bl = blue, pu = purple

3.1.5 Colour in Correlation with Shape

When one considers physical characteristics of flowers, such as effective corolla length or nectar sphere - sexual sphere distance, one may ask whether these features correlate with the bill length of flower visitors or with the coloration of flowers.

In this section I consider various features of flower colouring which may in turn be related to floral characteristics.

Fig. 8 shows the frequency distribution for corolla lengths of 1118 bird flowers from all over the world. The distribution is log-normal (mean 23.06 mm, S.D. 12.58 mm, Table 6.). The extremes are 3.5 mm and 130 mm corolla length. The different regions of the world show similar characteristics (Figs. 8 & 9) except where such a log-normal distribution is excluded by the special nature of the data base, as it is in Australia due to the low number of taxa (66), and in the Hawaiian Archipelago where the numerous subspecies of the Lobelioid flowers bring about a bimodal distribution. Australia has a very low mean, because flowers with long functional corollas are missing, whereas the Pacific Islands have the highest mean because of their predominantly long-tubed flowers.

Table 6 Mean corolla length of bird-pollinated flowers

Flowers	X	S.D.	N
New World	24.14	12.8	638
Old World	18.72	9.95	195
Australia	14.45	6.58	66
Hawaiian	28.05	14.88	218*
Archipelago			
all	23.06	12.58	1117

* Number of subspecies

Fig. 8

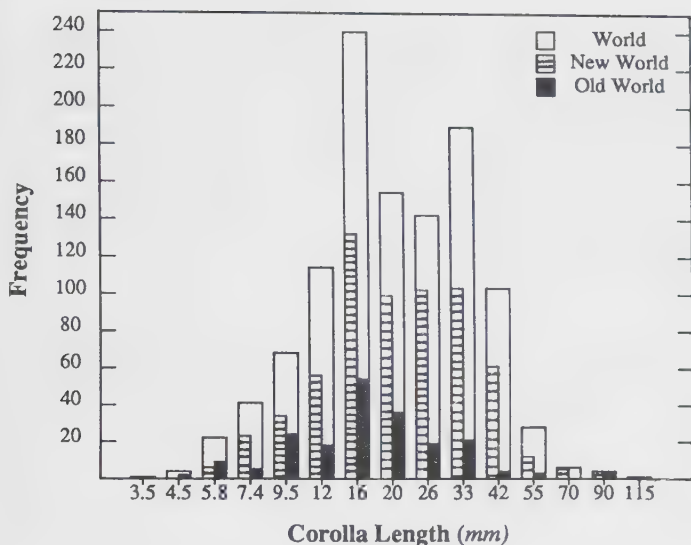
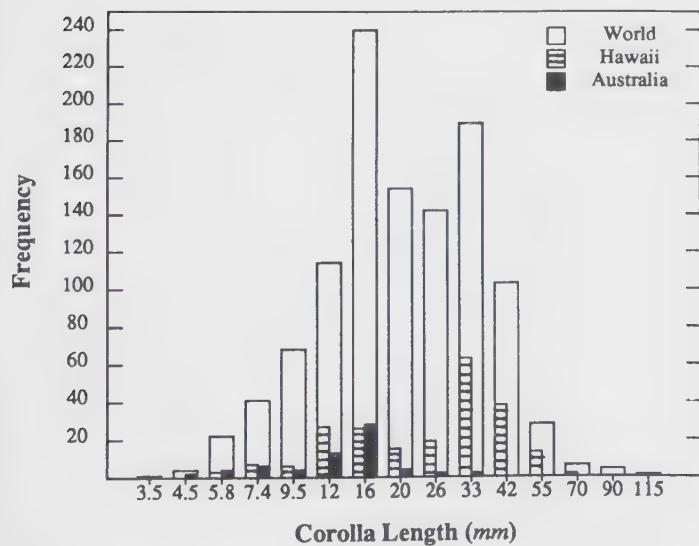


Fig. 9



Figures 8-9

Frequency distribution for corolla length, World, New World, Old World, Australia, and the Hawaiian Archipelago.

If one considers red and non-red taxa in two separate groups, a noteworthy distribution is obtained (Fig. 10). For the red-coloured flowers a unimodal distribution (mean 24.9 mm, S.D. 9.56 mm) results (Fig 10-a) but a bimodal distribution for non-red taxa (maxima at 15.4 and 33.2 mm; Fig. 10-b). The red and the non-red graphs are complementary in their minima and maxima. Red corollas are dominant when their lengths range between 16 mm and 26 mm; non-red corollas are dominant when shorter than 16 mm or longer than 26 mm. These two groups of flowers with either medium-sized or extreme-sized corollas show significantly different coloration ($\chi^2 = 215$, $p < 0.001$).

Similar graphs are obtained for the world's regions, separately considered (Fig. 11), except for the Australian non-red taxa which show unimodal instead of bimodal distribution.

Fig. 10

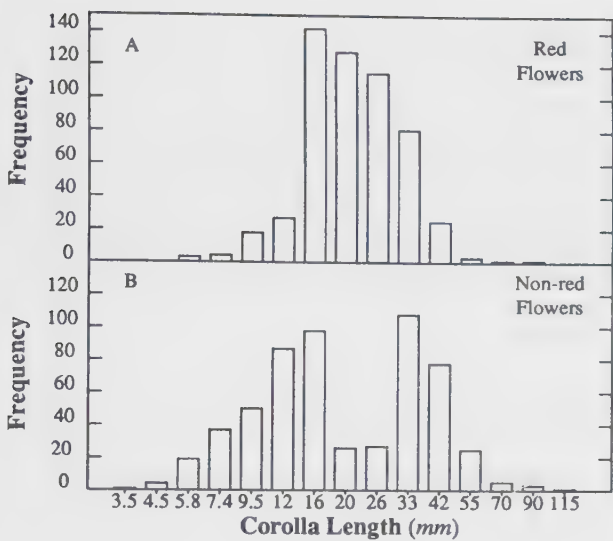
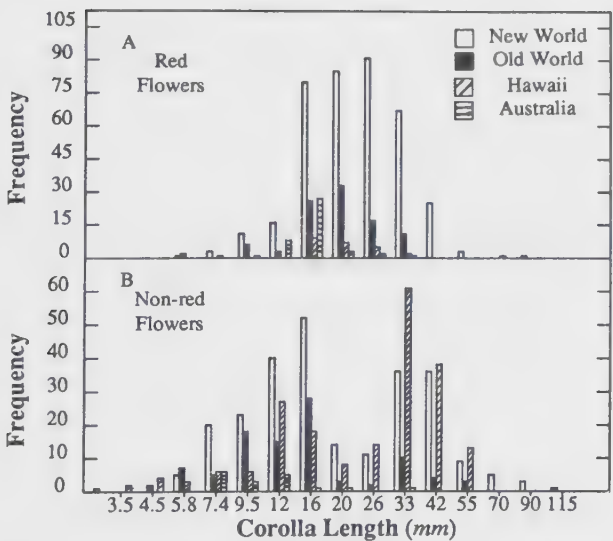


Fig. 11



Figures 10-11

10. Frequency distribution for corolla length of world's red and non-red taxa.

11. Frequency distribution for corolla length of regions' red and non-red taxa.

3.2 Classification of nectar-feeding birds

Nectar is consumed by many birds and the habit of nectar-collecting is obviously a polyphyletic one. Excluding hummingbirds, Fisk & Stein (1976) list 20 species of Northern American birds, in seven families, which have been observed feeding on nectar. However, the majority of nectar-feeders, and the most specialized ones, are concentrated in four families (Trochilidae, Nectariniidae, Drepanididae, and Meliphagidae, Table 7.).

Table 7. Characteristics of the four primary families of nectar-feeding birds.

Family	Number of species	Number feeding on nectar	Distribution	Range of bill length (mm)	Mean body weight (g)
Trochilidae	319	319	America	6-120	2.0
Nectariniidae	104	92	Africa, Asia	10- 42	6.9
Meliphagidae	167	167?	Australia	10- 35	8.5
Drepanididae	22	13*	Hawaii	9- 72	8.5

* of these, 6 species are extinct (Luther, 1972).

The data are compiled from:

Amadon (1950), Folger (1982), Grant and Grant (1968), Hall and Moreau (1970), Howard and Moore (1980), Luther (1972), and MacDonald (1973).

Nectar-feeding birds are among the smallest birds and the largest pollinators (Brown et al., 1978). The smallest nectar-feeding birds weigh 2g, the largest as much as 80g, and the vast majority of species weigh from 3 to 30 g (Table 7.). Besides body length, body mass, and coloration of plumage, the bill length (culmen length) is by far the most important ecological feature of nectar-feeding birds. The bill length exhibits considerable interspecific variation in all four nectar-feeding bird families. The range of bill lengths is widest in hummingbirds (Trochilidae), and Drepanididae (Table 7 & 8). A narrower range is found in sunbirds (Nectariniidae) and honeyeaters (Meliphagidae). The distribution is log-normal in Trochilidae (Fig. 12), and almost log-normal in Nectariniidae, but in Drepanididae it is bimodal (Fig. 13).

Unspecialized nectar-eaters with a mixed diet (fruits, fruit-juice, nectar, insects) such as flowerpeckers (Dicaeidae) and white-eyes (Zosteropidae) have a relatively short bill.

In hummingbirds and sunbirds the range of bill lengths is correlated with geographical latitude. (The lower the latitude, the broader the range, cf. sections 4.2 & 4.3).

Table 8. Mean bill lengths of nectar-eating birds

Bird Family	X	S.D.	N
Trochilidae	19.0	6.4	326
Nectariniidae	19.84	6.7	116
Drepanididae	20.33	10.78	45*
all	19.24	7.8	487

*Number of subspecies

3.3 New World nectar-feeding birds

3.3.1 *Hummingbirds*

The hummingbirds are unique in being the only group of nectar-feeding birds in the world which does not belong to the perching birds (Passeriformes) (Fig.14).

The highest density of hummingbird species occurs in the moist, open habitats of tropical and subtropical lowland. They are somewhat less common in tropical mountain forests, and are also found in moist temperate forests, and even in deserts.

Hummingbirds differ from other nectar-feeders in their capacity for sustained hovering flight, and for entering hypothermic torpor as a means of emergency energy conservation. Probably all hummingbird species feed on nectar. These birds generally possess thin straight bills. This would suggest an adaptation of the bill to their feeding behaviour (insects and nectar) during flight (Wagner, 1946).

3.3.2 *Migration*

Most hummingbird species are resident, spending the entire year in a single region (Grant and Grant, 1968; Linhart, 1973). However, the species of the family living on the southern and northern margins of the hummingbirds' distribution range (where flower nectar is only seasonally available) have acquired the migratory habit. The seven species of western North American hummingbirds mostly migrate northward to their breeding ranges in early spring as the flowering season commences, and return to their wintering ranges southward in late summer and early fall (Grant & Grant, 1968).

Fig. 12

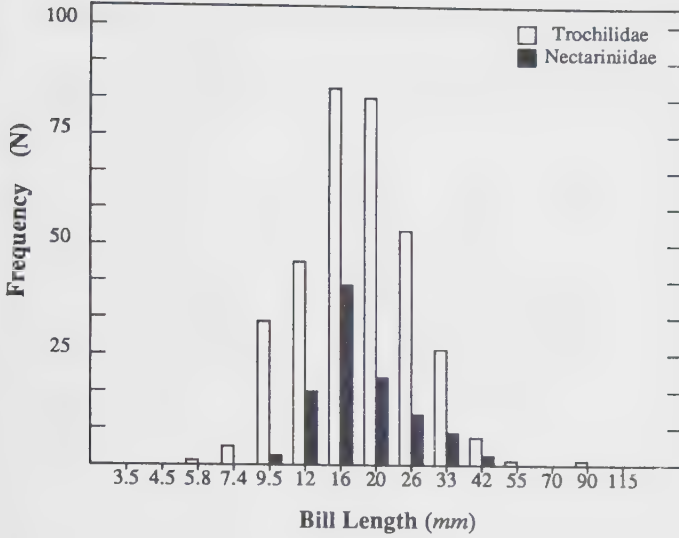
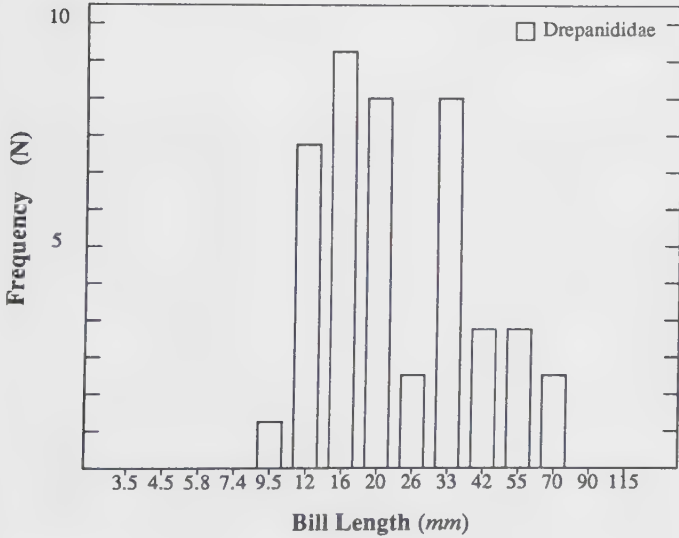


Fig. 13



Figures 12-13

12. Frequency distribution for bill length of Trochilidae and Nectariniidae.

13. Frequency distribution for bill length of Drepanididae.

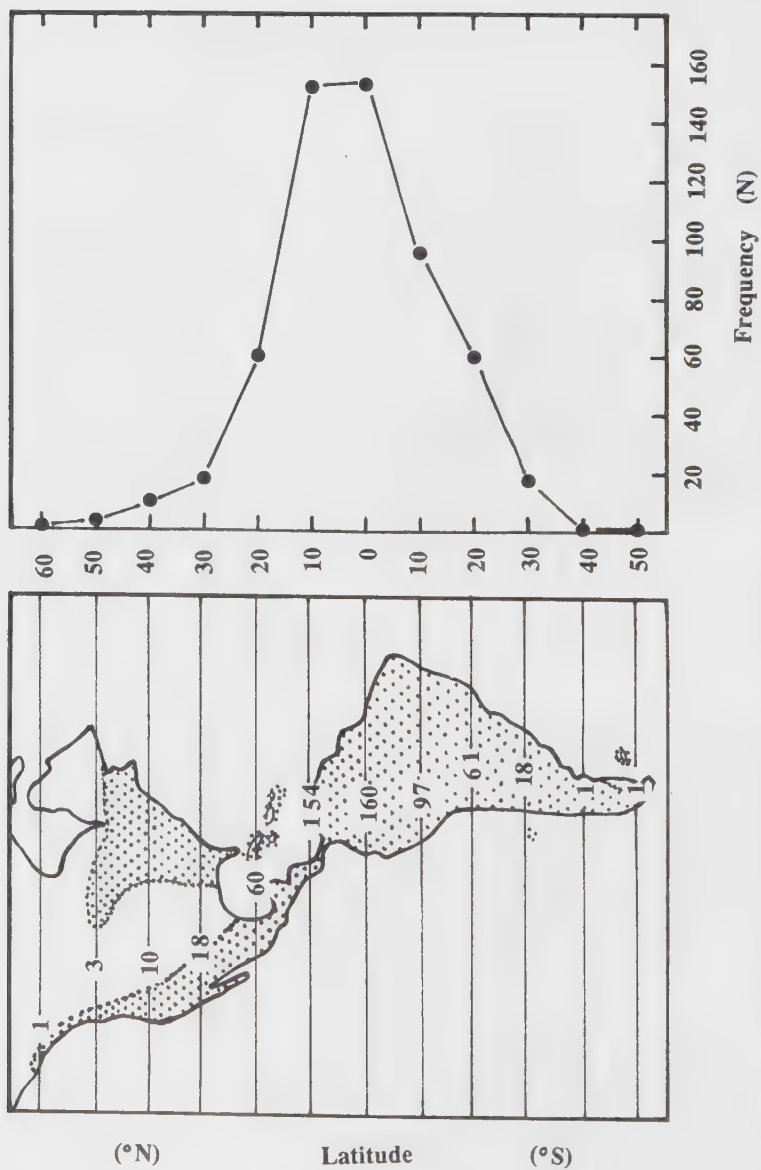


Fig. 14
Distribution and Frequency of Trochilidae. Reproduced from Grant and Grant (1968).

3.3.3 Territoriality

Hummingbirds of tropical and temperate habitats often defend their food plants and exhibit territorial behaviour.

Linhart (1973) distinguishes three types of territorial behaviour in hummingbirds:

- 1) Territoriality is most commonly noted in males of temperate and tropical species showing strong sexual dimorphism in coloration of plumage and/or body size.
- 2) Food-oriented territoriality by both sexes has been reported in species where both the sexes are equally showy in plumage and equally effective in their displays of territorial defense.
- 3) In the third group, called hermits, both sexes are uniformly dull plumaged, search widely for their food, and exhibit no territorial behaviour around a food source. These birds possess long, slightly decurved bills and are concentrated in the genera *Calypturus*, *Phaethornis*, *Threnetes*, and - with a strongly decurved bill - *Eutoxeres*.

Table 9. Behaviour of nine Central American hummingbird species.

Species	Bill Length	Behaviour
<i>Phaethornis superciliosus</i>	40.8	Hermit
<i>Eutoxeres aquila</i>	36.7	Hermit
<i>Threnetes ruckeri</i>	33.2	Hermit
<i>Glaucis hirsuta</i>	33.2	Hermit
<i>Chalybura urochrysa</i>	26.4	Non-hermit
<i>Amazilia tzacatl</i>	24.8	Non-hermit
<i>Thalurania furcata</i>	23.5	Non-hermit
<i>Florisuga mellivora</i>	23.4	Non-hermit
<i>Amazilia amabilis</i>	22.1	Non-hermit

After Stiles (1975)

3.3.5 *Passerine birds*

Passerine or perching birds which act as primary pollinators on New World plants have been observed by several authors (Feinsinger et al., 1979; Leck, 1974; Raven, 1974; Skutch, 1954; Steiner, 1979; Timkin, 1970; Cruden & Toledo, 1977). Six families including Thraupidae, Vireonidae, Icteridae, Mimidae, Coerebidae, and Psittacidae encompass most of the passerine nectar-feeding birds.

Such birds are not obliged to consume nectar since insects, fruits and fruit-juice constitute their main food. In tanagers (Thraupidae) and honeycreepers (Coerebidae) the bill is relatively unspecialized and short (10-12mm, Steiner, 1979). These birds prefer flowers with open-mouthed corollas and suitable means of support for their perching mode of nectar-consuming. Flowers which can be exploited in this way are relatively rare in the New World: only 12 of 64 New World species of *Erythrina* are adapted to perching bird pollination (Toledo, 1974); the remaining 52 species are hummingbird flowers.

3.4 Old World nectar-feeding birds

In the Afro-Asian continents there are three main nectarivorous bird families, the sunbirds (Nectariniidae), the white-eyes (Zosteropidae), and the flower-peckers (Dicaeidae), as well as less important families, such as Corvidae and Psittacidae.

The sunbirds inhabit a wide range from South Africa to North-East China and from West Africa to New Guinea and Australia. They live in all habitats of Africa except in the Saharan deserts. With their long, thin, and decurved bills and their sucking tongues they exhibit great adaptation to the nectar-providing flowers they live off. The features which distinguish sunbird species from each other are generally the shape of the bill, the length of the tail, and the amount of iridescent plumage. The species of *Anthreptes* with short, rather straight bills and more secretive habits behave exceptionally (Hall & Moreau, 1970). Birds classified in this genus feed almost exclusively on insects and spiders. Although the sunbirds number far fewer species (104) than the hummingbirds (319), the distribution curves of both families show similar characteristics. However, that for the former has a more gaussian shape than the latter. Due to the intervening Sahara belt in North Africa, in which sunbirds do not disperse, the distribution curve is asymmetric (Figure 15).

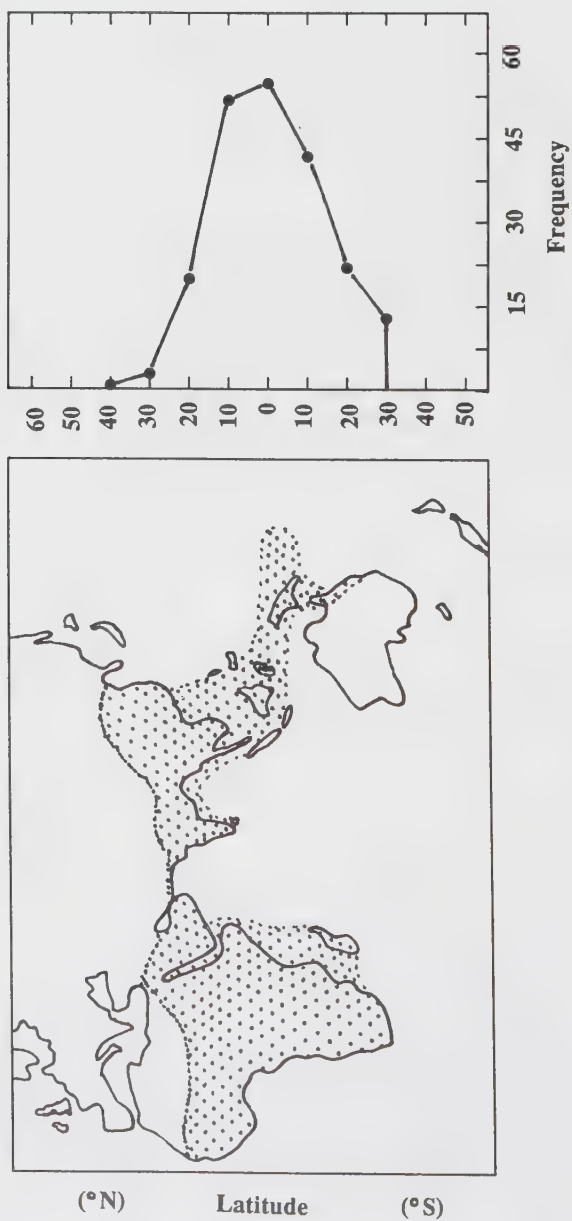


Fig. 15

Distribution and Frequency of Nectariniidae. Distribution reproduced from MacDonald (1973).

Another interesting fact is that the sunbirds do not disperse into the higher latitudes in Europe but do so in North China. In Europe, some bird-pollinated plants (introduced from elsewhere) and some indigenous plants are visited and pollinated by warblers (Sylviidae) and others (Ford, 1985). On the Canary Islands there are a few endemic bird-pollinated plants which are visited by Sylviidae (Vogel et al., 1984; Olesen, 1985).

3.4.1 The white-eyes

White-eyes (Zosteropidae) are relatively small birds with thin bills slightly decurved and sharply pointed. The range of their bill lengths is between 8 and 14 mm. Distributed round the periphery of the continent, they have brush-tipped tongues with which they extract nectar and fruit-juice, but they also feed on insects.

3.4.2 The flowerpeckers

Flowerpeckers (Dicaeidae) are found from India to Australia. The birds are small with short, square tails, and bills of varying lengths (6-11.5 mm). Members of the genus *Dicaeum* are mostly berry feeders.

3.4.3 The Honeyeaters

Honeyeaters (Meliphagidae) are numerous among Australian birds. The brush tongue, which is the principal feature shared by members of this family, is associated with the habit of eating nectar and also fruit or fruit juices. Their bill lengths vary from 10-35 mm.

3.5 Hawaiian nectar-feeding birds

The Drepanididae are a group of birds endemic to the Hawaiian Islands. These birds have exploited so many avenues and habitats that they can be called an outstanding example of adaptive radiation (Carlquist, 1980).

The Drepanidids can be divided into two subfamilies (Psittirostrinae and Drepanidinae, Table 11). In both subfamilies adaptive radiation has led to nectar eating behaviour (in the genera *Loxops*, *Hemignathus*, *Himatione*, *Palmeria*, *Vestiaria*, and *Drepanis*). Most of the species of *Loxops*, *Himatione*, and *Palmeria* have small beaks for probing through debris or shallow flowers in search of insects. The most common species of extant nectar-eating drepanidids are *Loxops virens*, *Himatione sanguinea*, and *Vestiaria coccinea*. On Mauna Loa their primary nectar sources in the spring and summer months are the brush-type inflorescences of the trees *Metrosideros collina* (Carpenter, 1976; 1978). *Vestiaria coccinea* has a medium-length bill (20mm) which allows feeding on shallow as well as on tubular flowers (*Clermontia arborescens*).

Long, tapering, curved bills are prominently represented in the genera *Hemignathus* and *Drepanis*. These birds feed on the long tubular flowers of the Lobelioids (Luther, 1972; Amadon, 1950; Carlquist, 1980).

Table 11. Hawaiian honeycreepers (Drepanididae).

Psittirostrinae			Drepanidinae		
Name	diet	bill length	Name	diet	bill length
Loxops			Himatione		
virens	i,n	13	sanguinea	n,i	10-12
parva	i,n	12	Palmeria		
sagittirostris	i,n	-	dolei	n	10-13
maculata	i,n	11	Ciridops		
coccinea	i,n	8	anna	f	
Hemignathus			Vestiaria		
obscurus	i,n	41-53	coccinea	n,i	20
procerus	i,n	47-52	Drepanis		
luicidus	i,n	25	pacifica	n,i	44
wilsoni	i		funerea	n,i	45-50
Pseudonestor					
xanthophrys	i				
Psittirostra					
psittacea	f,i				
contens	f,i				
bailleui	s,f				
palmeri	s				
flaviceps	s				
kona	s,i				
Melamprosops					
phaeosoma	-				

i = insects; n = nectar; f = fruits.

Data compiled from Carlquist (1980), Howard & Moore (1980), Luther (1972), and Amadon (1950).

4. RESULTS

Considerable variation is often evident in the birds' preference ratings for any given flower. The major sources of this variation are differences in bill dimensions, body size, relative dominance, and habitat preference among the hummingbird species of a community (Stiles, 1976).

The present and following sections are concerned with the relationship of the body size of hummingbirds to the corolla length of flowers.

4.1 Correlation of body weight and bill length

The correlates of body size variation are numerous and well documented (Brown et al., 1978). Nevertheless, their biological causes and consequences are often complex and poorly understood. Schuchmann (1979) and Leck (1973) noted that large hummingbirds living on islands in the West Indies possess comparatively long bills while small birds have short bills. There is a relationship between body mass and bill lengths in hummingbirds on these islands.

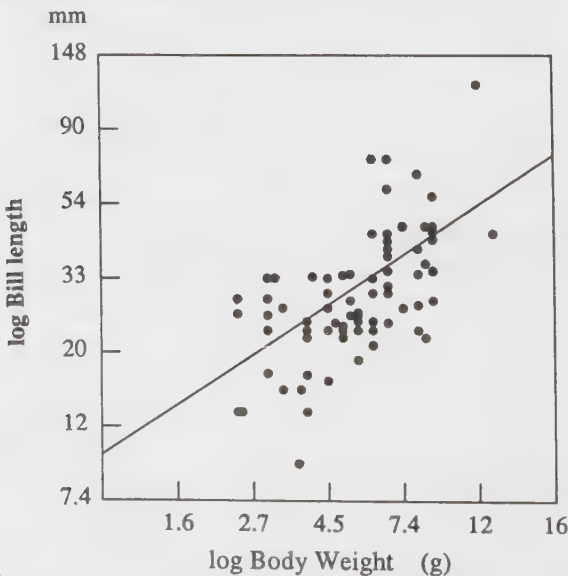


Fig. 16

Relationship between bill length (mm) of 88 hummingbird species and their body weight (g).

A general relationship between hummingbird bill length and body mass in 88 species is shown in Fig 16. The regression line is given by the equation:

$$\log \text{ bill length} = 2.31 + 0.674 * \log (\text{body weight})$$

In all cases correlation coefficients are significant at $p < 0.0001$. The correlation is moderate ($r = 0.656$).

4.1.1 Correlation of bill length and corolla length

When one considers physical characteristics of the nectar-secreting flowers, such as corolla length or the distance from the nectar sphere to the tube margin, one may ask how these features compare with those of the flower visitors. Hummingbirds of a given body and bill size should forage in such a way that their energy uptake is maximized relative to their energy expenditure (Stiles and Wolf, 1979; Carpenter, 1978). In a feeding experiment with artificial tubular flowers, Hainsworth (1973) demonstrated in two given bird species that the nectar intake decreases linearly with increasing tube length.

In this section I consider bill length as the trait of nectar-feeders which may be related in turn to corolla length.

A relationship between pollinator bill length and corolla length in 82 bird flowers of the New World is presented in Fig. 17. The exponential model is:

$$\log \text{ bill length} = 3.78 - 1.067 * \log \text{ corolla length} + 0.259 * \log (\text{corolla length})^2$$

Correlation coefficients are significant at $p < 0.0044$, $r = 0.803$.

The corolla length of a given food plant is on average 3-10 mm longer than the bill length of its pollinator (Fig. 18). This difference does not seem to be greatly influenced by absolute bill length.

Hummingbirds and their food plants fall into several size categories (Schuchman, 1978; Lack, 1973; Brown et al., 1978). Thus small-billed hummingbirds visit a set of flower species which have a comparatively short floral tube, and likewise large hummingbirds with long bills feed on a group of flower species with long corollas. Moreover, the small bird *Archilochus colubris* probes proportionally greater distances than the large bird

Lampornis clemenciae, though the latter is able to probe further in fact (Hainsworth, 1973; Fig. 17).

The probing distance of any given bird is composed of bill length and part of the tongue length. Hence it is scarcely surprizing that food plant corollas are longer on average than the bill of the relevant pollinator (Fig. 18). In large birds, the probing distance is determined more by bill length than by tongue length, while the contrary is true with regard to smaller birds (Hainsworth, 1973). This may account for the non-linear relationship in bill and corolla lengths (Fig. 17), and for the fact that the difference between corolla and bill length is not dependent on bill length.

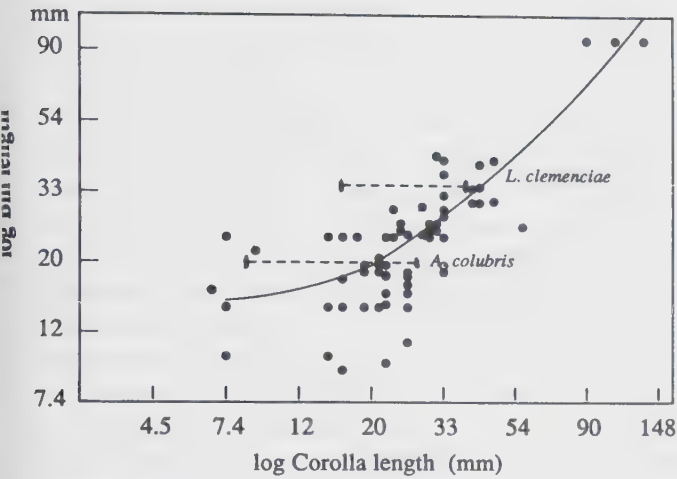


Fig. 17

Relationship between bill length (mm) of hummingbirds and floral tube length (mm) of their food plants. Dashed lines indicate ranges of observed food plant sizes for *Archilochus colubris* and *Lampornis clemenciae*.

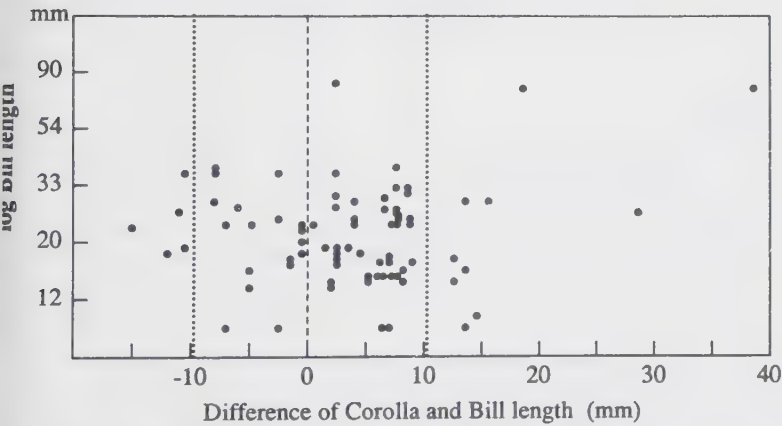


Fig. 18

Scatter diagram of bill length (mm) vs difference of corolla and bill lengths for American hummingbirds and their food plants.

4.2 Colour Distribution

Waser (1983) maintains that flower colours have somehow evolved to maximize the coverage of the pollinator visual spectra, and to minimize competition within plant species, when their density is high. Weevers (1952) found no substantial variation in the proportion of flowers of various colours in temperate and tropical latitudes, despite different pollinator faunas (Waser, 1983). However, Weevers did not treat colours of bird-pollinated flowers separately.

This was done by Pickens (1941, 1955) and Grant (1966, 1968) in Western North America and in southern Mexico, respectively. There seem to be little or no differences in colour between the hummingbird flora of California and that for Central and South America, judging from Melin's (1935) colour data from the border areas of Argentina and Bolivia (Crosswhite and Crosswhite, 1981). Most of the colours were red, orange, yellow, or white to the human eye.

The primary and secondary colours of 1113 bird flowers of the world show similar distribution when scattered in a two-coned colour space (Fig. 19). Despite the fact that these plants grow in different countries of the world, the colour variety increases proportionally to the number of flowers investigated. Colours are not uniformly scattered in the space: the green segment is almost empty (minimal contrast to leaf colours) whereas the density in the red segment is high (best contrast to leaf colour). The colours are mainly saturated (1072). Of the non-saturated colours, white is the most abundant (186).

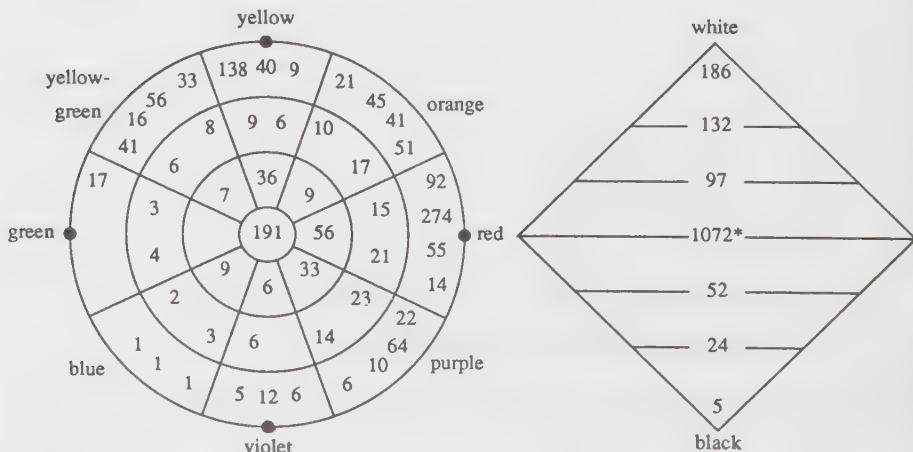


Fig. 19

Scatter diagram of corolla colours of 1113 bird flowers of the world (apical and frontal view of colour space). (* saturated colours)

4.3 Initial model concerning the coloration and shape of bird flowers.

Floral odours and floral colours generally serve to attract animal pollinators from a distance, while floral foods stimulate repeated visits to the flowers once the food source is discovered (Grant & Grant, 1968). Odours are frequently lacking on bird flowers. But birds do discriminate between colours. The commonest colours of the world's bird-pollinated flowers are various shades of red. Red is at least as conspicuous to birds as it is to humans (Chen et al., 1984), and, by contrasting with the green background, it serves to attract birds from a distance. Furthermore red is the only colour of the spectrum which is inconspicuous to most insects: for bees it is nearly black, and even hawkmoths prefer lighter colours to red in twilight (Paige & Whitham, 1985).

Red flowers have an maximum frequency when their effective corolla length ranges from 16 to 26 mm (Fig. 20). The bill lengths of their legitimate bird pollinators correspond with these lengths (Figs. 17 & 18).

Red flowers often have markings which serve as nectar-guides and enable birds to find the entrance more quickly. For reasons of maximal contrast with flower and leaves, such guides should lie at mid-distance between red and green in a colour space. Four possibilities are conceivable. In the chromatic dimension these are yellow and blue-violet; in the achromatic dimension, black and white (Fig. 21).

A relatively long narrow corolla tube is an excluding factor for competitor bees whose mouthpart lengths lie out of the range necessary for good access to red bird flowers (Table 10). A further limiting factor for hawkmoths is that the rhythm of nectar secretion in bird-pollinated flowers is diurnal, whereas that of hawkmoth flowers is nocturnal. Though moths can reach the nectar chamber of bird flowers with their proboscises, they may find it empty in late evening hours.

If the density of bird flowers increases, the red flag colour should be diversified to take maximal advantage for one or more pollinators. This should be a non-red colour. Where the yellow and blue-violet parts of the spectrum are occupied by the coloured nectar-guides of red flowers, orange, yellowish-green, bluish-green and purple are potential alternatives. For reasons of contrast, the achromatic colours white and black also belong to this group of non-red flowers. Their effective corolla lengths are either short or long, and are comparable to the corolla lengths of bee and hawkmoth flowers, respectively (Fig. 22). Also in this group, the bill lengths of their legitimate bird pollinators correspond with the corolla lengths.

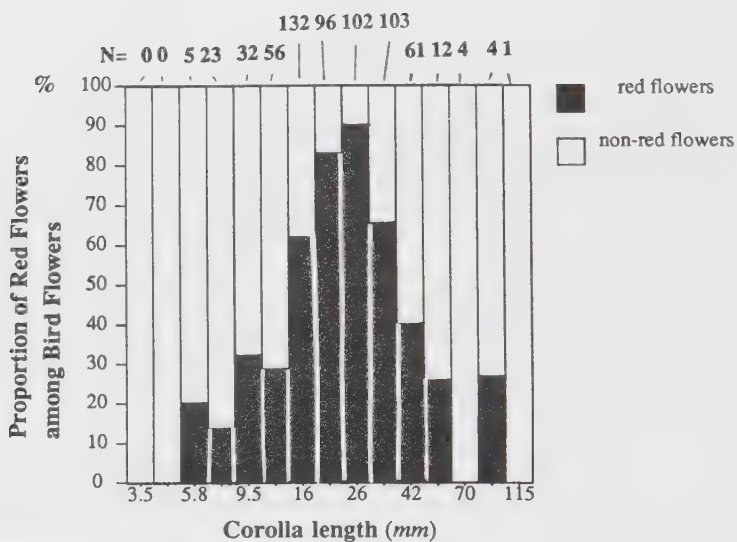


Fig. 20

Distribution of red and non-red bird flowers of the world at different corolla lengths.

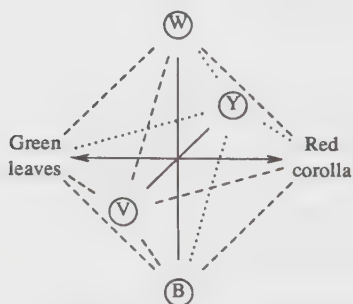


Fig. 21

Colour space. Red corolla as a maximally contrasting colour to green leaves. Yellow (Y), violet (V), white (W), and black (B) as postulated nectar-guide colours with maximal contrast to both the red corolla and the green leaves.

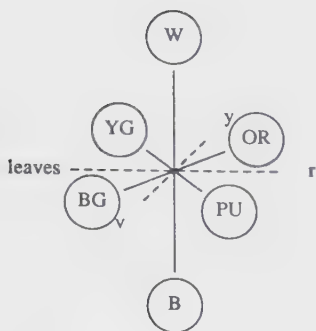


Fig. 22

Colour space. Possible flower colours, when abundance of bird flowers is high. White (W), Orange (OR), Purple (PU), Black (B), Blue-green (BG), and Yellow-green (YG).

Summary

The pollinator systems of nectarivorous birds and bird flowers show similar empirical regularities all over the world as regards coloration of flowers, corolla lengths, and bill lengths of the pollinators. One may distinguish between two categories whose ecologically relevant pollination traits complement each other in several respects: in coloration of flowers, in tube length, and in bill length.

One category is characterised by red flowers with medium corolla lengths which are frequented by common birds of medium bill lengths. Nectar-guide colours of these flowers show maximal contrast to the main coloration (red) and the green leaves.

The second category represents non-red flowers with short or long corolla tubes, which are visited by birds of correspondent bill lengths. Also non-red flowers possess nectar-guide colours which contrast best to their basic colours.

Transitional forms between these two categories are very likely to occur. They may indicate an evolutionary tendency in bird flowers.

4.4 Testing the model on the world's taxa of bird flowers

Red bird flowers may possess coloured nectar-guides. To achieve maximal contrast, such colours have to be as far from green and red as possible in colour space. As already mentioned, yellow, violet, white, and black are contrasting colours in precisely this way. Fig. 23 shows the nectar-guide colours of red flowers in colour space. The bright colours yellow and white are very common, violet and black less so. Red flowers possess predominantly the above-mentioned nectar-guide colours, whereas non-red flowers have yellow-green, orange, blue, purple, yellow, and white as secondary colours.

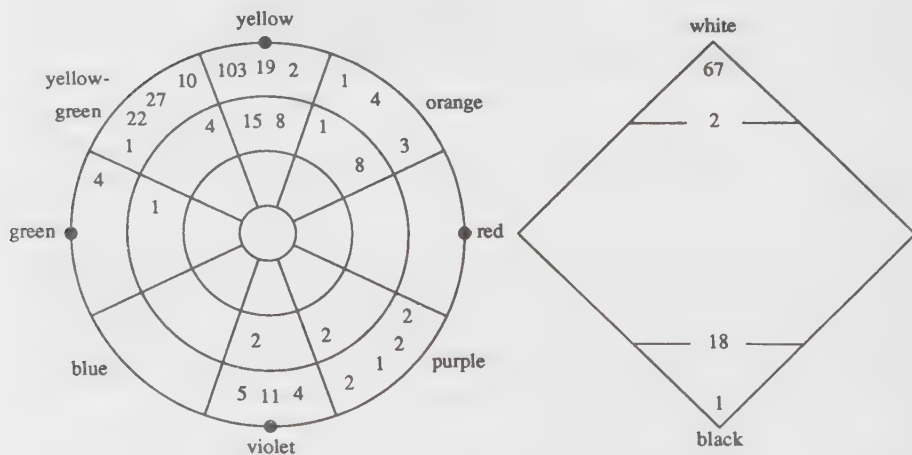


Fig. 23

Colour space: Nectar guide colours of red bird flowers. Its frequency is high in saturated yellow and nonsaturated white. A less dense distribution is seen in violet and black.

Red bird flowers are reported to have medium corolla length. A confirmation of this floral trait is presented in Fig. 24 (Red 9-12). The distribution of corolla length with red hue is unimodal.

Bird flowers with long and short floral tubes are restricted in colour to the following segments: orange, yellow-green, blue, purple, white, and black. Yellow and violet bird flowers can not be assigned to any class of corolla length (cf. Fig. 24).

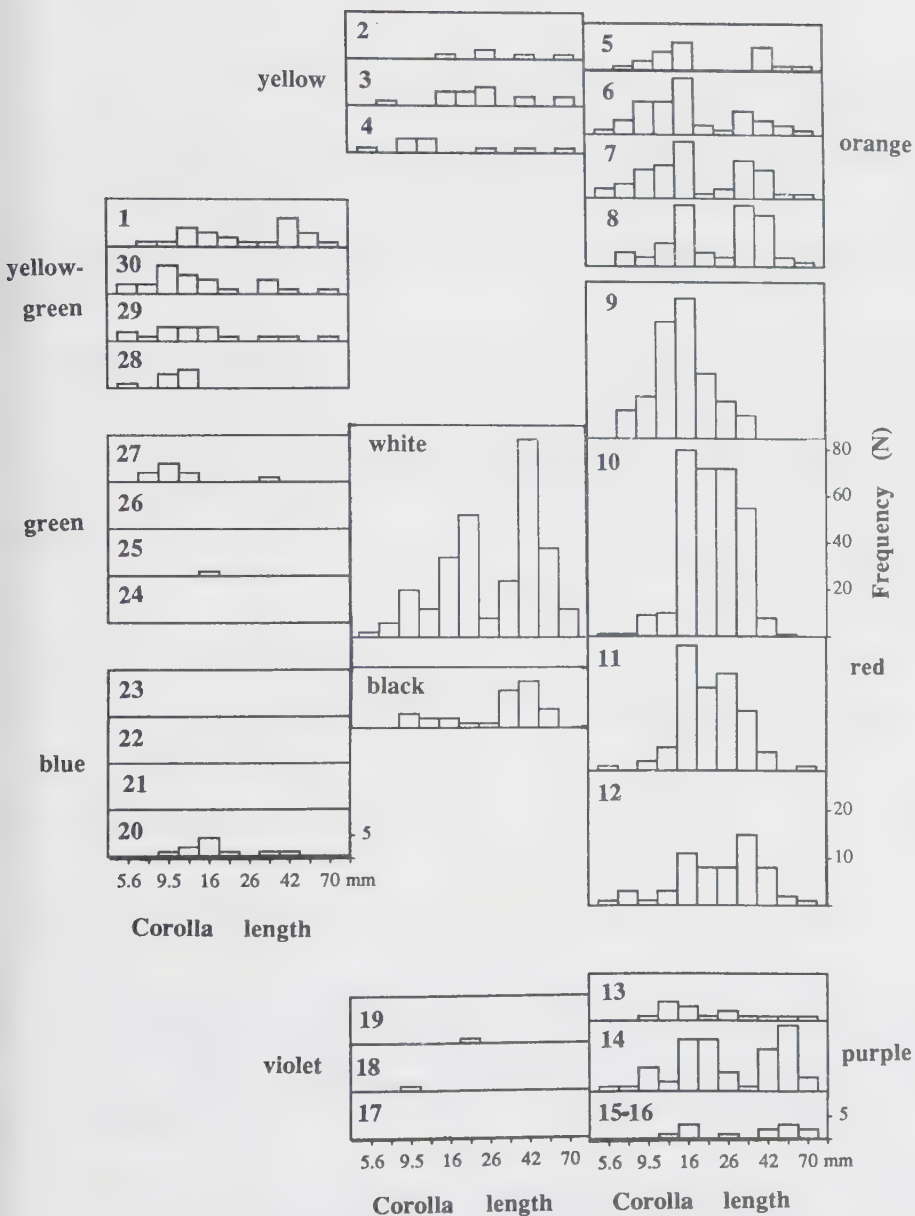


Fig. 24

Frequency for corolla length in the 32 hue distinct subgroups of world bird flowers. Yellow-green, green, blue, purple, orange, white, and black flower groups are bimodally distributed, the red group is log-normal.

4.4.1 Taxonomic groups

The 1113 investigated taxa belong to 56 families. However, families with over 100 taxa are scarce. Of the families with the most taxa, only four are suitable for statistical investigation viz.:

the Campanulaceae-Lobelioideae (315 taxa), the Leguminosae (135), the Scrophulariaceae (115), and the Onagraceae (100).

Lobelioids are rather common in the New World tropics and on the Hawaiian Islands. In the genera *Pratia*, *Siphocampylus*, *Lobelia*, *Heterotoma*, *Sclerotheca*, *Delissea*, *Cyanea*, *Rollandia*, *Clermontia*, *Centropogon*, *Burmeistera*, the syndrome of ornithophily is known (Carlquist, 1980; Vogel, 1980). Bird-pollinated Lobelioids have a fourfold variation in flower colours. Fig. 25 presents the distributions in the colour diagrams.

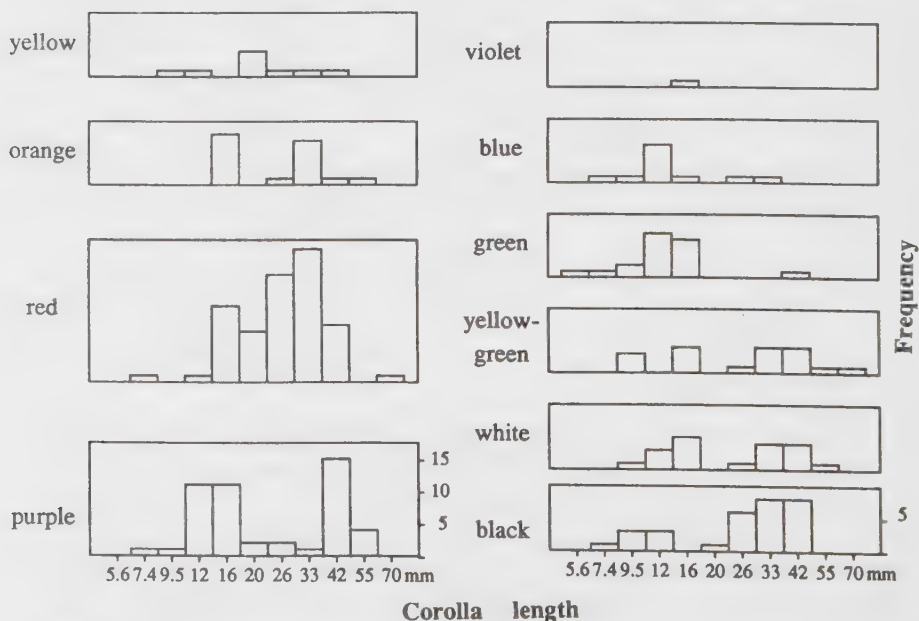


Fig. 25

Frequency for corolla length in Lobelioid bird flowers (world-wide).

As expected, the frequency of the group of red flowers is highest and exhibits unimodal distribution with a peak at medium corolla length. But orange, purple, blue, green, yellow-green, white, and black coloured flower-groups demonstrate bimodal distribution.

The family Leguminosae is extant in all terrestrial habitats and has much of its diversity concentrated in areas of varied topography with seasonal climates (Polhill et al., 1981). The 135 investigated taxa belong to 26 genera, including *Erythrina*, whose 107 species are bird-pollinated (Raven, 1974; Toledo, 1974). Although this genus has spread all over the world and is adapted to both perching and hovering modes of exploitation, most of the taxa are restricted to the yellow-red segment in floral colours. In the remaining genera blue, yellow-green, black, and white flowers occur rarely.

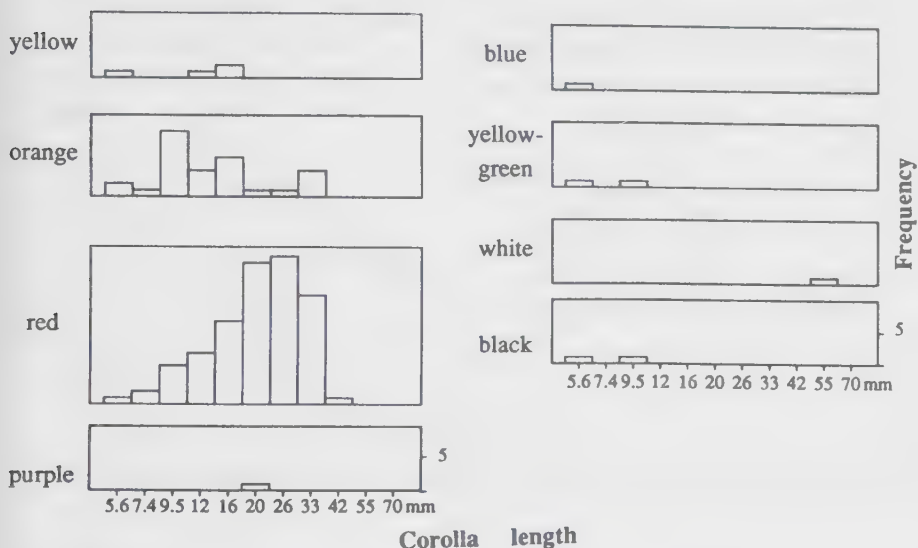


Fig. 26

Frequency for corolla length in Leguminosae bird flowers (world-wide).

As in the Lobelioideae, red flowers also predominate in the Leguminosae and yield a typical, unimodal distribution. For orange flowers a bimodal distribution is suggested, whereas the counts in the blue, yellow-green, white, and black segments are too few to show the mode of distribution, although long- and short-tubed species indicate bimodal spread (Fig. 26).

The Old World species are pollinated by perching birds, especially by members of families such as Nectariniidae, Sturnidae, and Oriolidae (Ali, 1931; Docters van Leeuwen, 1932; Porsch, 1924; Singh, 1929; Guillardmod et al., 1979). The vast majority of New World species are pollinated exclusively by hummingbirds (Hernandez and Toledo, 1982); a dozen species are pollinated by passerine birds (families Icteridae, Parulidae,

Thraupidae, Coerebidae, etc.) (Cruden and Toledo, 1977; Feinsinger et al. 1979; Morton, 1979; Steiner, 1979, Toledo and Hernandez, 1979).

The sunbirds and the hummingbird feed mostly on red flowers whereas the perching birds feed on species with short gaping corollas of orange or yellow-green coloration.

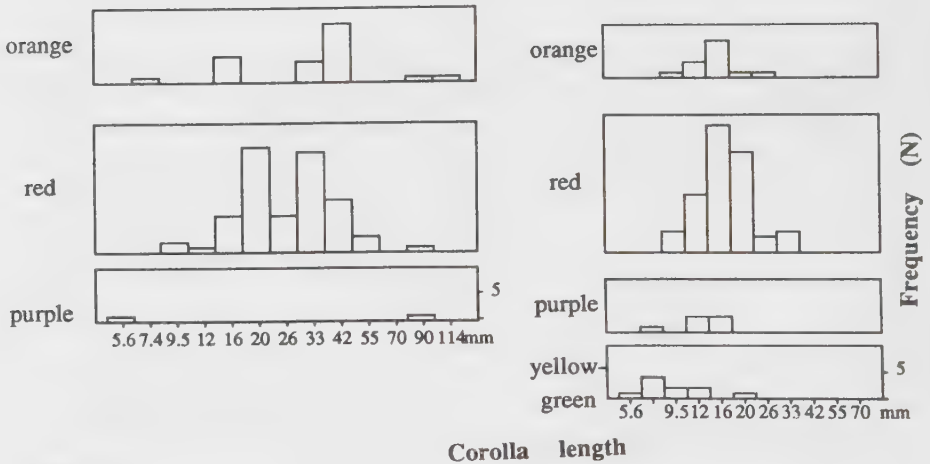


Fig. 27

Frequency for corolla length in Onagraceae (left) and in Scrophulariaceae bird flowers (right).

The families Onagraceae and Scrophulariaceae both have many species in the New World, and both exhibit little colour diversity. Orange, purple, and green colours are much less frequent than red.

4.4.2 Colour Variants

Flower colours within a single bird flower species may vary geographically. Waser (1983) suggested that *Ipomopsis aggregata* flowers vary in colour and corolla length in a seemingly arbitrary manner as a function of the local colour environment.

According to the model the probability for a flower to be red is closely related to its corolla length (Fig. 20). To test this, colour varieties in the 1113 investigated taxa were

sought. 14 species were found whose varieties show geographically distinct colour morphs. Each of these species exhibits a red beside a non-red variety. The non-red varieties are white, purple, or orange.

The 28 varieties are graphed in a histogram (Fig. 28). The graph showing the distribution of red and non-red flowers at different corolla lengths (circles) serves as a comparison. According to this graph species with 16 mm and with 35 mm corolla lengths occur equally likely with red than with non-red flowers (dashed lines at the 50% level). Around these points colour varieties also are most abundant. This suggests an adaptation by bird flowers to these special circumstances. At these points none of the colour varieties (red or non-red) has a selective advantage over the other. As a result, both forms persist.

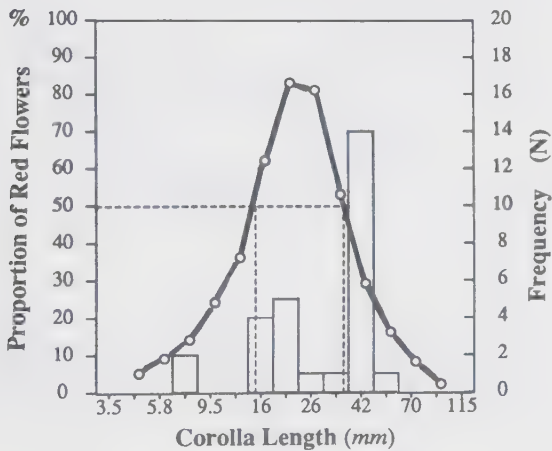


Fig. 28

Distribution of corolla lengths of 14 species for varieties in flower colour (histogram) in comparison with the proportion of red and non-red flowers at different corolla lengths (circles). The frequency of colour varieties is highest around the 50 % level (half of taxa red, half of taxa non-red in colour).

4.5 Testing the model on New World taxa

The previous section (4.1) deals with the relationship of body size and corolla size in the flower pollinator interaction. In this section geographical latitude is also taken into account.

If one considers that the distribution and frequency of bird flower species is somehow related (Fig. 11), one may ask whether there is a relationship between abundance of species, diversity of bill length, and latitude of the habitat of birds in the New World. This is displayed in a two-way histogram (Fig. 29) where the y-axis represents the latitude and the x-axis the classes of bill lengths. Maximal diversity and density of species coincide: most species live around the equator and these are highly diverse with respect to bill length. In addition to an abundance of birds with medium-length bills, we also find the bird with the longest bill (*Ensifera ensifera*) together with short-billed species (*Ramphomicron* spp., *Orthorhyncus cristatus*).

Towards higher latitudes in both the northern and the southern hemispheres, birds with extremely long bills do not occur, whereas birds with medium-sized bills are still present.

An analogous graph is presented for the 638 investigated bird flowers of the New World (Fig. 30). Again maximal diversity is seen in the tropics (+25 to -25 degrees), and lower diversity towards higher latitudes.

It now becomes clear that the distribution of birds and flowers is geographically correlated. In hummingbirds and their food plants three size categories are discernible: Small-billed birds which forage on non-red, short-tubed flowers, medium-billed birds which feed on red flowers, and long-billed birds feeding on non-red, long-tubed flowers.

Field observations of the feeding-behaviour of hummingbirds should indicate the same tendency. From the data set of Snow & Snow (1972), I compiled the proportion of red to non-red flowers of the food plants for nine hummingbird species (Fig. 31) living in a Trinidad valley. The percentage of red flowers visited by each of the nine birds (bars) is then clearly correlated with the distribution of red and non-red bird flowers at different corolla lengths (circle) in the New World. Birds which feed in the shorter corolla range feed predominantly on the non-red group; birds which feed in the medium-length feed on the red group.

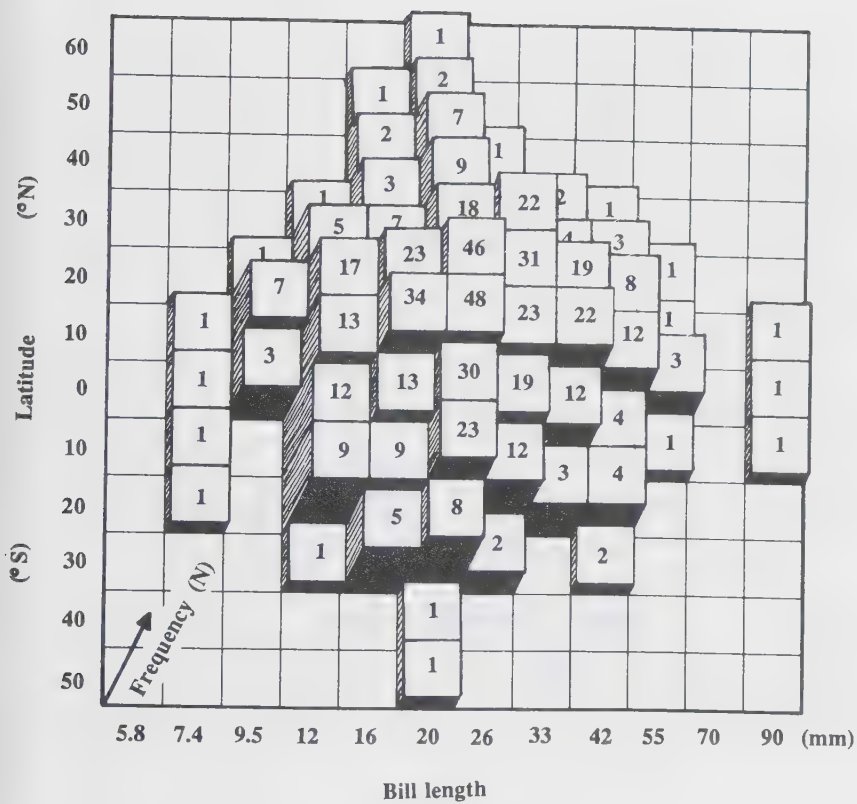


Fig. 29

Frequency of bill lengths at different latitudes in New World hummingbirds.

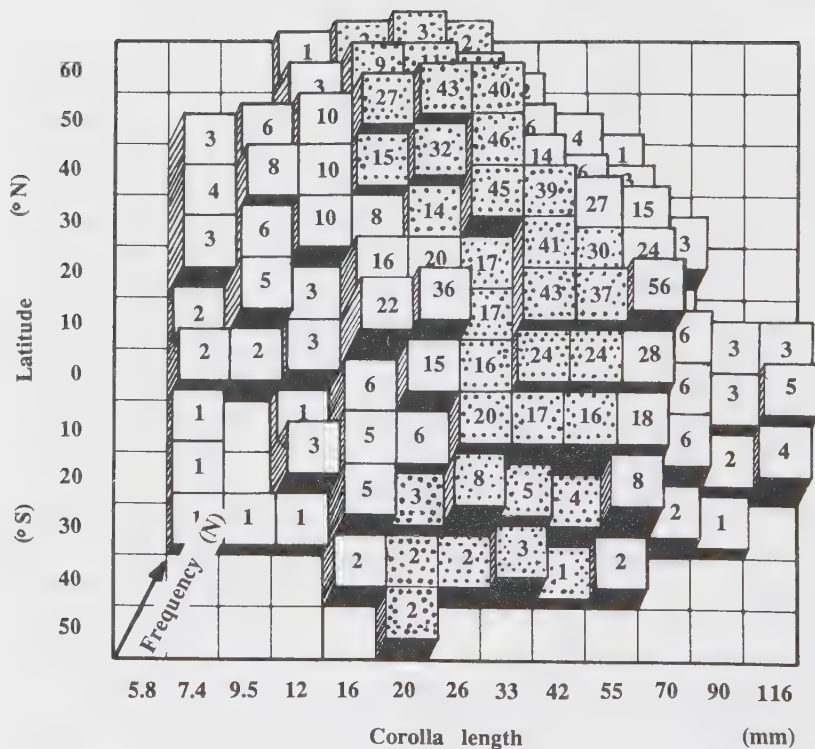


Fig. 30

Frequency of corolla lengths at different latitudes in a sample of 637 New World bird-pollinated species.

- ▨ predominantly red flowers
- predominantly non-red flowers

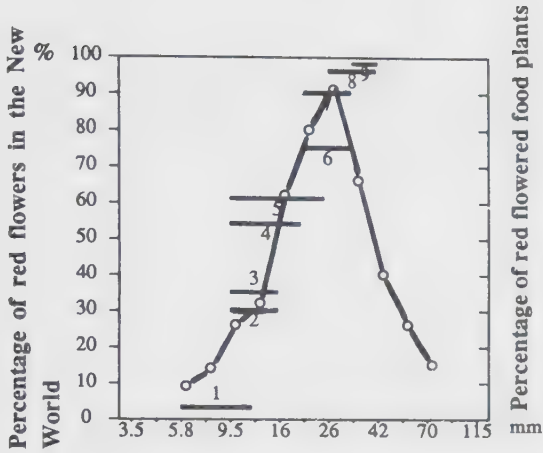


Fig. 31

Percentage of red-flowered food plants and range of their corolla lengths for nine tropical hummingbird species (1-9) in comparison with the percentage of red flowers of varying corolla lengths in the New World (circles). 1 = *Chrysolampis mosquitos*; 2 = *Chlorestes notatus*; 3 = *Saucerottia tobaci*; 4 = *Amazilia chionopectus*; 5 = *Anthracothorax nigricollis*; 6 = *Phaethornis longuemareus*; 7 = *Florisuga mellivora*; 8 = *Phaethornis guy*; 9 = *Glaucis hirsuta*. Bars indicate range of food plant tube size. (Data from birds from Snow & Snow, 1972; percentage of red flowers of varying corolla lengths, this study).

New World bird flowers have a rich array of floral colours. Beside the abundant red flowers, orange, yellow, purple, violet, blue, green, yellow-green, and white floral colours have been recorded. They show the familiar distribution characteristics (Fig. 32).

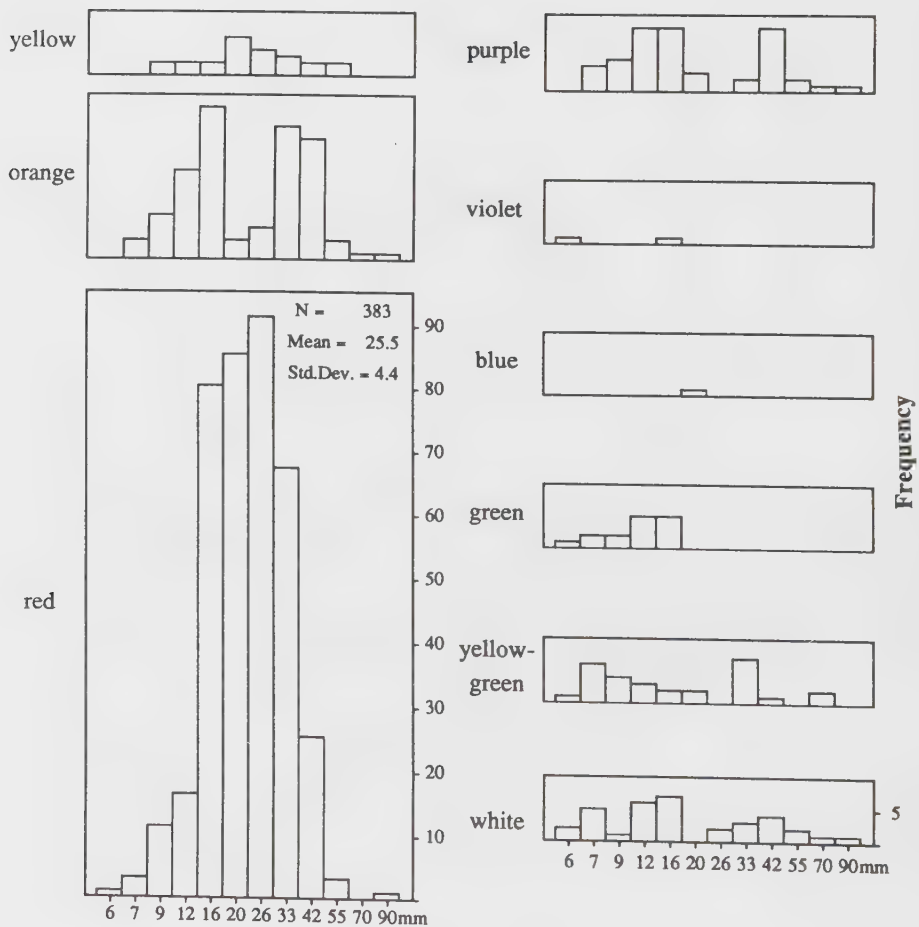


Fig. 32

Frequency of corolla length and colours in New World bird flowers

4.6 Testing the model on Old World taxa

The Old World sunbirds (Nectariniidae) are essentially ecological equivalents of the New World hummingbirds (Trochilidae) (Wolf & Wolf, 1976). In Fig. 33 high diversity in bill length coincides with the tropics and decreases toward higher latitudes. The distribution of bird flowers follows similar patterns.

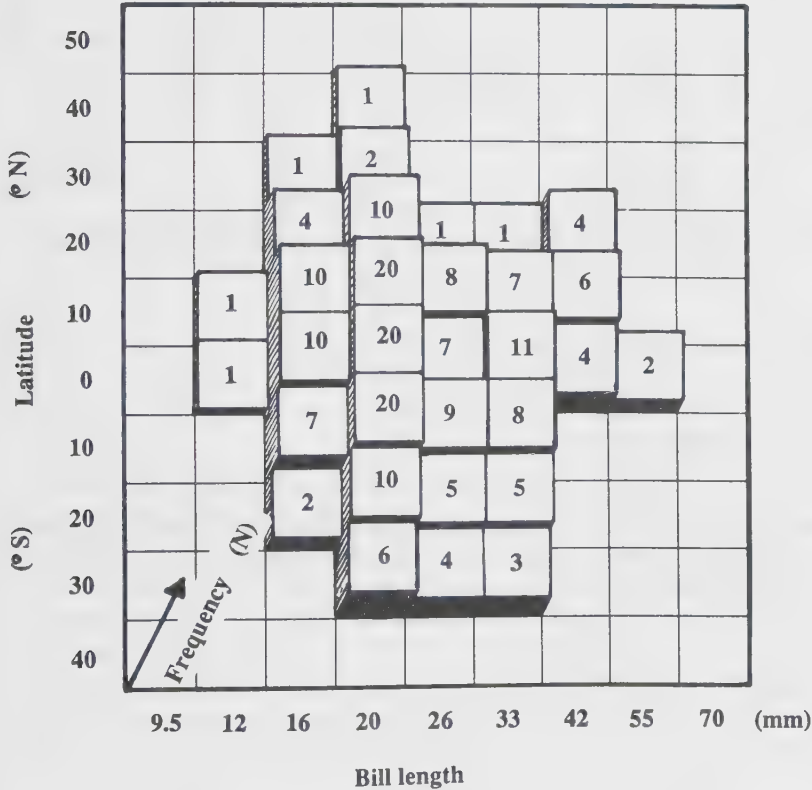


Fig. 33

Frequency of bill length at different latitudes in Old World sunbirds (Nectariniidae).

In Old World flowers red flowers are again abundant and typically log-normally distributed; non-red flowers are bimodal (Fig. 34).

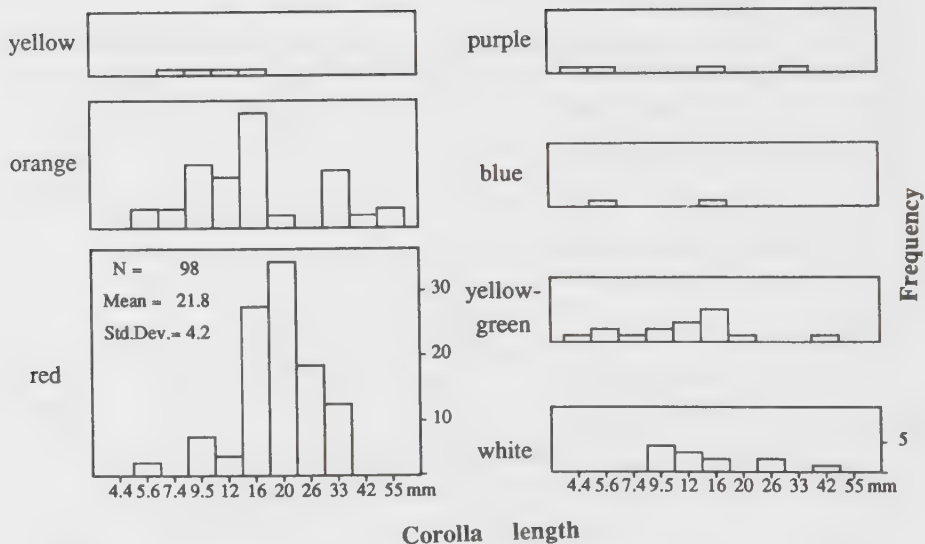


Fig. 34
Frequency of corolla length and colours in Old World bird flowers.

4.7 Testing the model on Australian taxa

Australia has red flowers with medium corolla lengths. In my sample of over hundred bird flowers the non-red flowers belong all to the small size class and not to the class of flowers with long effective corolla lengths.

4.8 Testing the model on Hawaiian taxa

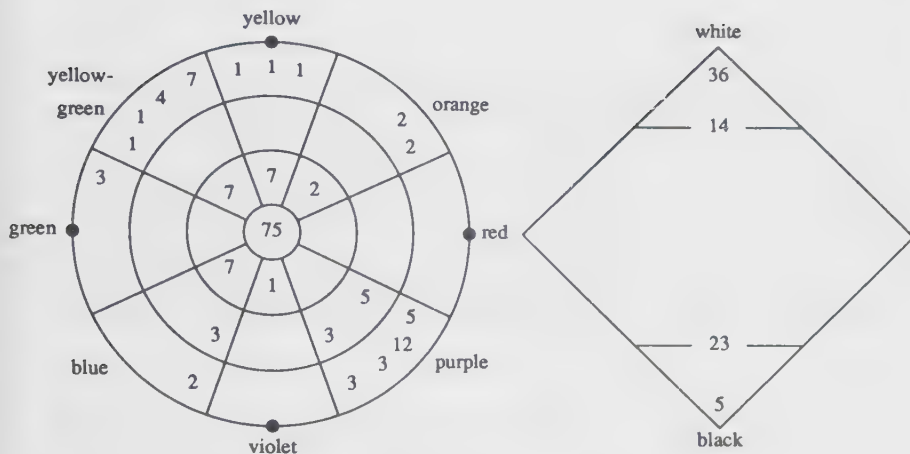


Fig. 35

Diagram of corolla colours of Hawaiian non-red flowers (apical and frontal view of colour space). Colours are concentrated in the three complementary segment pairs orange-blue, purple-yellowgreen, and white-black.

In the Hawaiian islands, *Metrosideros* plants constitute the red flower group almost exclusively. Orange flowers, which are otherwise very common throughout the world, are scarce on these Pacific islands. Non-red flowers are amply represented and yield a typical bimodal distribution (purple, blue, green, yellow-green, white, as well as black). In colour space the non-red flowers belong almost entirely to the three complementary pairs, orange - blue, purple - yellow-green, and white - black (Fig. 35). The Drepanidid birds - both extant and extinct - altogether exhibit a wide bill length variety. Corolla variety is also high. These variations are closely comparable to those of the birds and flowers found at the same latitude (20 north) in the New World.

4.9 Discussion

Body size - Bill size - Corolla size

Body size and bill length are important traits in hummingbirds. Body size, especially the bill size, influences foraging behaviour and has direct consequences for ecological and evolutionary relationships among nectarivores and plants (Brown, et al., 1978). Large birds have long bills and probe flowers with long floral tubes (Figs. 16 and 17). Medium-sized and small birds possess short bills and feed on the nectar of flowers with medium-length or short corollas, respectively. For the smaller size categories correlation with corolla length is loose, however, because their tongues disproportionately increase the effective probing distance compared to those of birds with long beaks (Hainsworth, 1973).

Brown et al. (1978) stated that, when floral nectar is equally available to animals of different body size, the small nectarivores keep the standing crop of available nectar so low that larger animals could not forage profitably and are competitively excluded. Furthermore, Lack (1973) noted that small flowers produce just enough nectar to support small, but not large, hummingbirds. However, I could not find a general relationship between corolla length and the amount of nectar secretion in 60 investigated plants ($r = 0.023$, data from literature) of the New World. This is probably due to the fact that some investigated taxa with open-mouthed short corollas secrete large amounts of nectar. But these particular species are visited by passerine birds with high body masses and energy expenditure, not by small hummingbirds.

Plants which utilize large pollinators have evolved long floral tubes to prevent consumption of their nectar by small nectarivores. Where several species of nectar-feeding birds coexist in the same habitat they often differ in beak size and tend to subdivide the bird-pollinated plants on that basis. Interspecific competition is thereby minimized. As a result, communities of plants and nectar feeders are organized in part according to pollinator mouthpart size (Feinsinger and Colwell, 1978). On islands which harbour few coexisting bird species, a subdivision of flowers within one bird species is effected by sexual dimorphism in the bill size of males (territorialists) and females (trapliners) (Wolf, 1975).

Hummingbirds fall into several size categories. In the tropics the maximal number of categories occur, while the number diminishes towards temperate latitudes (Fig. 29). In

the latter regions birds with extreme bill size seem to be competitively excluded by the hawkmoths with their long mouthparts, and by bees with their short proboscises (Table 10). Competitive exclusion between insects and birds is only one factor in accounting for the dropping out of these birds in passing from the equator to more temperate latitudes. Food availability may be another factor accounting for this distribution. Large size and the lower temperature results in high energetic demands on the birds (Hainsworth & Wolf, 1972). Large birds need large quantities of nectar offered by long-tubed flowers daily. Such nectar sources from flowers which fit their beaks closely, are lacking in temperate latitudes, or else the nectar is only seasonally available. Moreover, short- and long-billed hummingbirds have achieved a plant-pollinator specificity and are very adept hermits. These characteristics contrast with those of birds which are not strongly nectarivorous (Zosteropidae, Dicaeidae) and show no significant variation of bill size with latitude.

Small-to-medium sized birds (having beaks within the 16 to the 20 mm range) are most abundant throughout the entire distribution area (Fig. 29). The birds of this group are generalists who feed on an array of flowers which fit their beaks closely, but they also feed on unspecialized flowers in competition with insects (Grant & Grant, 1968; Snow & Snow, 1972; Feinsinger & Colwell, 1978; Stiles 1976).

Although the sunbirds number far fewer species than the hummingbirds, their distribution has similar patterns (Fig. 12), with a decline in bill variation toward temperate latitudes (Fig. 33).

Nectar-guides

Bird flowers possess coloured patterns which are thought to serve as nectar-guides.

In a series of experiments Waser and Price (1981) determined that rare plants of *Delphinium nelsonii* (a bumblebee flower) with albino flowers are undervisited by hummingbirds and bumblebees as compared with the normal blue forms. The basic reason appears to be that pollinators take longer to manage to extract nectar from albino flowers because these lack the strongly contrasting nectar-guides found on normal blue flowers (Waser 1983). It seems that no similar observations have yet been carried out on red and non-red bird flowers, although the contrastingly pigmented parts found around the entrance of floral tubes have been interpreted as nectar-guides (Werth, 1915; Toledo & Hernandez, 1979).

Red flowers have a variety of possible guide colours (Table 5). Though practically all

colours occur, the most common are yellow, white, black, and violet, colours which contrast maximally to the red floral body and the green leaves (Fig. 23).

Non-red flowers are not inferior in the diversity of possible colour variants for their nectar-guides (Table 4.). These flowers too have colours which bring about maximal contrast to the flower or to flower and leaves together (Table 4). Black and white contrast is found in white, black and purple flowers, colour contrast in orange and blue flowers.

This accords well with what was postulated earlier by the initial model.

Evolution - Coevolution

It is argued that birds have relatively little impact on the coloration of flowers (Waser, 1983). What, then, dictates variation in colours? The most plausible explanation is that in the evolution of a predominantly red hummingbird-pollinated flora in temperate North America, the initiative has fallen to the plants (Goldsmith et al., 1979).

It is important to realize that the environment presents species with a challenge, but the species itself determines in which way it will respond to that challenge (Campbell, 1985). Different species will respond to a common environment in different ways. This is true also for ornithophilous plants, except that parallel evolution has led to similar syndromes of bird flowers all over the world. With little local diversity (straight or decurved tube, the lack of colour or tube length classes in some places), bird flowers as a whole demonstrate the same types of regularities or trends. Plants which have evolved polyphyletically and separately on the Hawaiian islands and flowers from the New or Old World belong to the red floral class when they are common, have tubes of medium length, and are pollinated by generalists. Plants with flowers of the non-red class are either frequented by uncommon birds such as hermits and passerines with long beaks, or their floral tubes are short, and they are pollinated by unspecialized passerines or non-migratory birds with short beaks, and are limited mostly to the tropics. These two extremes of bird flowers contrast in size as well as in colours.

It is hard to believe that this law-like relationship recognized by me for the first time, which is clearly demonstrated by ornithophilous plants and their pollinators, could have been brought about exclusively by variation and natural selection. Natural selection is strictly a local mechanism and hence inherently unable to account for any global trend or pattern (Ho and Saunders, 1984). This relationship is not deterministic in all its

refinements, however, since bird flowers always have alternative pathways for adaptive evolution. These include several equivalents in nectar-guide colours for red flowers (Fig. 23), and several equivalents for the primary colour in non-red flowers (Fig. 35). Alternative pathways might be responsible for patterned variation in floral colours, e.g., the two colour variants within a single individual of *Erythrina oliviae*, whose flowers are orange buff or yellow-green (Krukoff & Barneby, 1974), or the long, decurved lobelioid flowers whose colour forms are white or black (*Cyanea rollandioides*), and yellow-green or purple (*Clermontia arborescens*).

These examples may indicate that bird-pollinated plants have a high plasticity in coloration and have a potential for shifting and evolving colours. Thus, individual populations of *Ipomopsis aggregata* shift to lighter red corolla colour during the flowering season which coincides with the emigration of hummingbirds from the system. In the absence of hummingbirds, the flowers with lighter colours attract hawkmoths (Paige & Whitham, 1985). Gottsberger and Gottlieb (1980, 1981) have shown that blue flowers occur predominantly in herbaceous angiosperms. In bird flowers a given floral colour is not restricted to a woody or a herbaceous form. However, the colour is strongly dependent on the plant family the plant species belongs to. The subfamily Lobelioideae exhibits by far the most diverse bird flower colours of all plant families where bird pollination is known.

Flower colour is largely due to the presence of pigments in chromatoplasts or cell vacuoles (Harborne, 1982; Kay et al., 1981). The most important of flower pigments are the flavonoids since they contribute cyanic colours (orange, red, blue) as well as yellow and white (Harborne, 1982). Other groups are carotenoids and chlorophylls, which provide principally yellow and green colours. In the case of cyanic colours, there are three main pigments of anthocyanidins: pelargonidin (orange-red), cyanidin (magenta), and delphinidin (mauve). These differ in structure only in the number of hydroxyl groups in the B-ring. These three chromophores occur, usually singly or occasionally as mixtures, in angiosperm flowers (Harborne, 1982; Gottsberger, 1971). All pink, scarlet, and orange-red flowers contain pelargonidin, most crimson and magenta flowers cyanidin, and all mauve and blue flowers delphinidin. This proves to be the case for the *Mimulus cardinalis* complex, where the insect-pollinated *M. lewesii* contains only cyanidin in its petals, whereas the bird-pollinated members of the same complex contain both pelargonidin and cyanidin (Vickery, 1978). Evolution of flower colour is caused by mutation of cyanidin to pelargonidin or delphinidin according to Harborne (1982).

Conclusion

Although there are striking differences between passerine and non-passerine bird flowers and pollinators (van der Pijl, 1937; Raven, 1974; Toledo, 1976; Cruden and Toledo, 1979) plant-pollinator communities are organized so as to exhibit similar patterns all over the world. These include the effective floral tube length and its coloration, as well as the beak length of the relevant pollinators. Thus the syndrome of bird pollination should include non-red short- and long-tubed flowers which are visited by birds of appropriate bill lengths, in addition to red tubular flowers of medium length, visited mostly by generalists. Bird flowers showing transitional stages between red and non-red flowers also exist (examples p. 63). The coevolution of birds and plants seems to be non-specific which is the rule in most plant-pollinator communities (Gilbert, 1980). This self-organization of these communities is caused by competition and cooperation among their members tending towards or maintaining optimal states for each member in a given environment.

An interpretation of evolutionary trends in some bird flowers of Western North America follows in the final chapter.

5. EVOLUTIONARY TRENDS IN BIRD FLOWERS OF WESTERN NORTH AMERICA

5.1 Evolutionary trends from insect flowers to red bird flowers

The bird flowers of western North America occur in a wide variety of ecological habitats, including desert, arid woodland, mountain forests, and coastal and arid scrub communities (Grant & Grant, 1968). In the southern area, a greater abundance of hummingbirds is undoubtedly the primary factor responsible for the occurrence of relatively numerous species of bird flowers in the same area (Grant & Grant, 1968). In the northern area, a manifest decline in the abundance of both bird-pollinated plants and nectarivorous birds has been documented (Figs. 29 & 30) (Crosswithe and Crosswithe, 1981).

There are strong indications that most species of hummingbird flowers have evolved from insect-pollinated ancestors (Grant, 1968). They may be derived from bee, hawkmoth, butterfly, and fly flowers (Grant & Grant, 1968; Grant & Grant, 1965).

As shown earlier, the mean bill length of hummingbirds is exceedingly different from those of the bees' and hawkmoths' mouthparts (Table 10). I consider these relations of the mean mouthpart lengths of the three animal classes to be conservative and not to have changed greatly since the era of the early nectarivorous birds. Hummingbirds are relatively recent intruders into temperate latitudes. According to Axelrod (1973), the topographical and climatic changes that occurred during the latter half of the Tertiary, gave rise to the Mediterranean Scrub vegetation of the latter half of the Pliocene. It is tempting to speculate that some migrating bird species penetrated from the tropics into higher latitudes. These generalists with medium to small bill sizes (16-20 mm) would have intruded into an insect-pollinated flora and fed on the flowers of these plants.

An array of plants would have been available to them, by virtue of existing floral structures, viz. those which matched most closely the final syndrome of medium-sized bird flowers. These ancestors would have been predominantly sympetalous Dicotyledons with the syndrome of a bee flower. For instance, the tubular flower of *Penstemon* sp. (Fig. 36) has different effective corolla lengths for bees and birds. The bees, with their short proboscises, are forced to enter the corolla while probing for nectar. This contrasts with the mode of probing by birds, whose bill length best fits the corollas, enabling them to feed on nectar simply by inserting their beaks into the floral tube. To exclude competitive

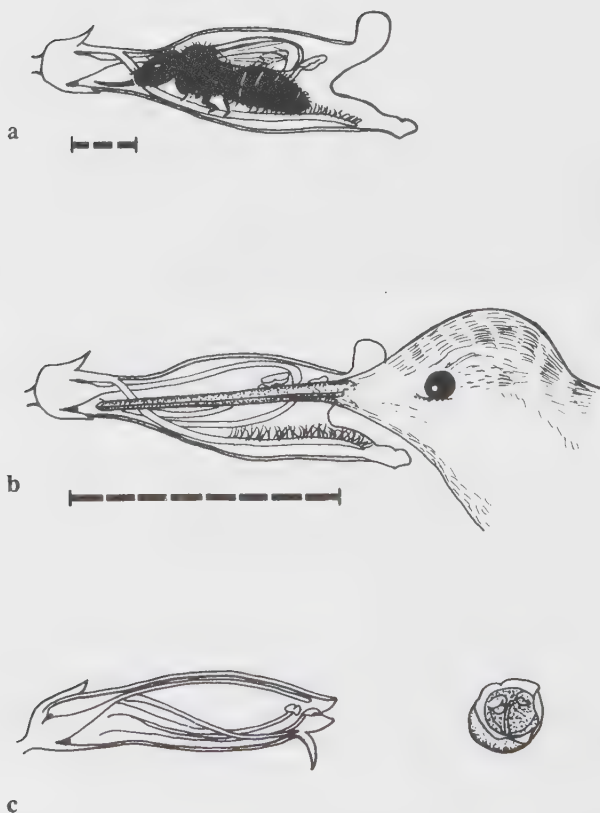


Fig. 36 a-c)

- a-b) Different effective corolla lengths of the bee flower *Penstemon rupicola* (Scrophulariaceae), for a bee (a) and a hummingbird (b) as visitors (hypothetical cases). The two agents use different mouth-part lengths when feeding on nectar (dotted lines).
- c) *Penstemon centranthifolius*, a bird flower of the same length, but with distinct narrow tubular corolla for excluding bees.

The drawings are based on living plant materials and on preserved animal bodies.

bees, the corolla tube of the bee flower would have become narrower, the flower coloration red, and the flower would have eventually produced large amounts of dilute nectar.

Most taxa in the genus *Penstemon* could have become adapted to birds according to the pattern described above. Several species, however, among them *P. newberryi*, show a transitional stage, since they diverge from the syndrome of a bee flower and approach, but do not fully attain, the typical condition of hummingbird flowers. For instance, *P. newberryi* has a rose-red corolla 18-19 mm long and bearded ventral ridges (Fig. 37). These ridges are interpreted as vestigial bee nectar-guides. Insect guides may change into bird nectar-guides during phylogeny. Ridges thought to be derived in this manner can be seen on the lower lip of the bird flower *Justicia californica* (Acanthaceae).

During my stay in California, I did not have an opportunity to observe any hummingbirds probing on *Penstemon newberryi*. In a population near Camino Campground, Madera county, carpenter bees (*Xylocopa californica*) and bumblebees (*Bombus sonorus*) were observed in the rôle of nectar thieves. As the narrow floral tube does not admit them inside to obtain the nectar legitimately, the insects were piercing the corolla for it (Fig. 37).

Transitional stages were also found in the genera *Stachys*, *Salvia*, and *Trichostema* (Labiatae). Compared to the closely related *Trichostema parishii*, *T. lanatum* has a larger flower with much more exerted stigma and anthers to facilitate nototribic pollination by hummingbirds (Grant & Grant, 1968; Spira, 1980). The blue-violet flower possesses an insect nectar-guide (Fig. 38). Blue-violet bird flowers are extremely rare (Tab. 3), whereas this colour is frequent in bee flowers. According to the author's hypothesis it is tempting to speculate that the blue floral colour of *T. lanatum* will shift towards red as the corolla tube (actual size 6-7 mm) increases in size. But field data revealed no significant range of variation in tube length. Only a trend towards the disappearance of the nectar guide was observed. Along Mulholland Rd., Los Angeles County, half of the flowers investigated lacked the white nectar-guide pattern. By contrast, this guide was never missing in the bee flower *T. parishii*, where it is a functional cue.

The flower of *Salvia spathacea* is also derived from a bee flower, as is clear from the presence of the no-longer-functional lever mechanism, an invention of the bee-pollinated *Salvia* species (Fig. 38). With its purplish-red coloration and its effective corolla length of 16 mm, this species resembles a non-red bird flower.

Stachys chamissonis flowers, of rose-purple coloration, are larger than the bee flower of

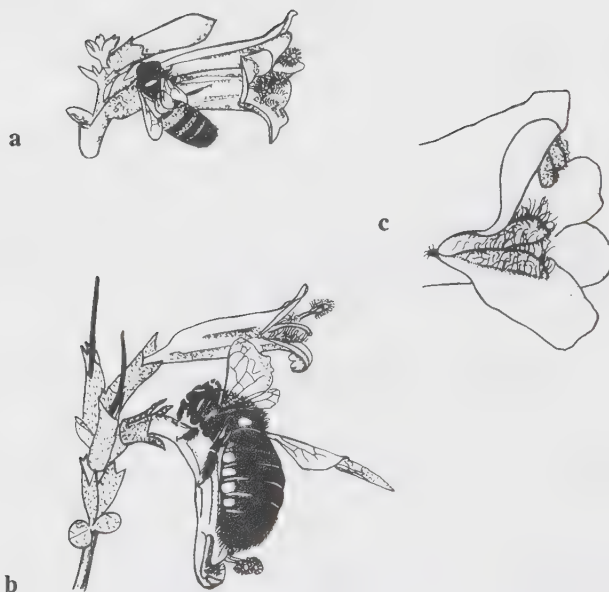


Fig. 37 a-c)

Penstemon newberryi. a) Carpenter bee (*Xylocopa californica*) and bumblebee (*Bombus sonorus*) (b) as nectar thieves on flower of *P. newberryi*, transitional between the syndromes of bee and bird pollination. It has bearded nectar-guide ridges (c) typical of bee flowers, but it also has a bee-excluding, narrow floral tube.

(These drawings based on author's photographs).

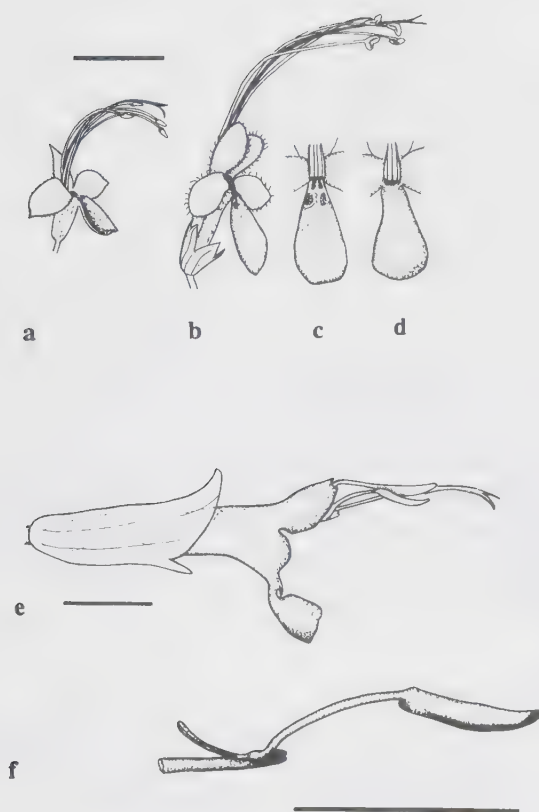


Fig. 38 a-f)

Trichostema parishii. (a), *T. lanatum* (b-d), *Salvia spathacea* (e-f). The anthers and stigma of *T. lanatum* are much projected compared to those of the bee flower *T. parishii* and guarantee nototribic pollination by birds. The nectar-guide is sometimes lost (c-d). The flower of *S. spathacea* (e) includes a no-longer-functional lever mechanism (f). Bars indicate 1 cm. The drawings are based on wild plant materials collected in California.

St. bullata, but the corolla is not narrow enough for excluding bees.

All these above-mentioned species are ecologically similar to non-red bird flowers of the small-size category but exhibit an evolutionary trend toward larger-sized, red bird flowers.

Hummingbirds of more extreme size categories appear at lower latitudes with warmer climates in America. I suggest that early evolution of bird pollinator and plants emerged in similar patterns: The medium-sized birds and flowers became established first, followed by the more extreme size categories.

This process has not stopped since. Six bird species migrate through the Colorado Desert and along the Pacific slope in late winter and spring to their various breeding regions. In the post-breeding summer season, many of them ascend into the higher mountains (Sierra Nevada or Rocky Mountains) and later migrate southward into Mexico. Anna hummingbirds (*Calypte anna*) and the island race of Allen hummingbirds (*Selasphorus sasin*) are the only non-migratory hummingbirds in California (Grant & Grant, 1968; Stiles, 1973). Although the Anna hummingbird is resident in Central California, many individual birds ascend to higher elevations in the mountains in the post-breeding season. Anna hummingbirds also occur in NW Baja California, Mexico (Howard & Moore, 1980). This suggests an earlier migratory route of this species from Mexico to California and back, which may have altered recently due to a warmer climate which could have led to this disrupted distribution.

The *Mimulus calycinus* complex

Hawkmoth flowers generally have longer tubes than red bird flowers. If a hawkmoth flower evolves into a red flower, its corolla has to become shorter.

For instance, lighter colour variants of *Ipomopsis aggregata* exhibit a gradient of increasing corolla length, with significant differences between the red bird-pollinated morphs and all other colour variants that are hawkmoth-pollinated (Student-Newman-Keuls Multiple Range Test, $p < 0.05$) (Paige, pers. comm.).

A species complex in which the corolla gradually decreases in size from a hawkmoth to a bird flower, is described below.

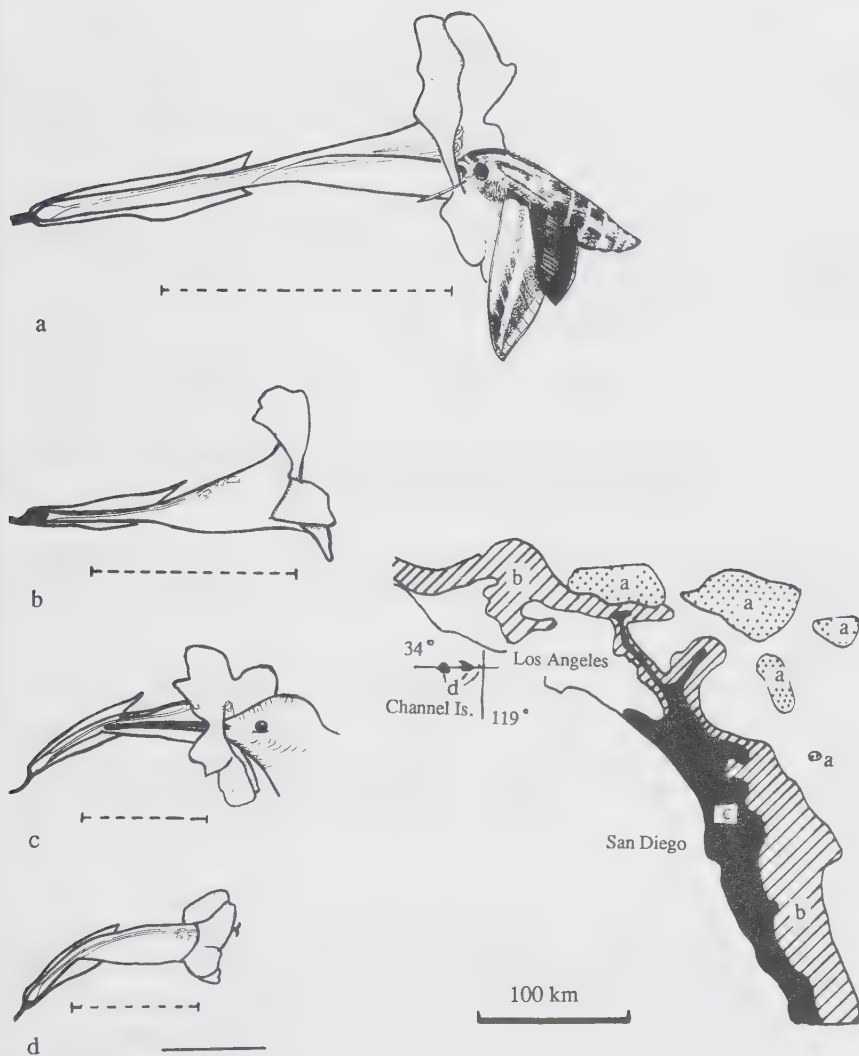


Fig. 39

Clinal size variation and distribution in flowers of the *Mimulus calycinus* complex.

a) *M. calycinus*, b) *M. longiflorus*, c) *M. puniceus*, d) *M. flemingii*. *M. calycinus* is hawkmoth-pollinated, the three remaining taxa are bird-pollinated. The floral tubes and throats decrease gradually in size from *M. calycinus* to *M. flemingii*.

Dotted lines indicate the effective corolla lengths, bar indicates 1 cm.

Distribution map reproduced from Beeks (1962), the drawings are based on flowers collected in the field, the hawkmoth and the bird are reproduced from Grant & Grant (1965).

Beeks (1962) described a complex including several taxa on the mainland of southern California, which are transitional to each other. The three main population systems include *Mimulus calycinus*, *M. longiflorus*, and *M. puniceus* (Fig. 39), and since they hybridise partially but not fully, such a system is called a semispecies (Grant, 1963).

This complex has its centre of diversity in the summer-dry vegetation of California. The generalized habitats for the three *Mimulus* species are the habitat for *M. puniceus* along the West coast; the adjacent hillside habitat for *M. longiflorus*; and farther east the rock crevices habitat for *M. longiflorus* (Fig. 39).

M. calycinus has a very long, cream-coloured corolla with a long, straight, narrow tube which abruptly expands into a throat. The colour is of a pastel yellow, ivory, or creamy hue. Pollinators are the golden-blue fly *Eulonchus smaragdinus* and the hawkmoth *Celerio lineata*; less frequent visitors are hummingbirds.

M. longiflorus has an intermediate corolla and a slightly angled tube. The salmon-orange flowers of variable colour intensity are visited by hawkmoths and hummingbirds.

M. puniceus has a corolla throat and tube of equal length, the corolla tube being curved and short. The principal pollinators of the red flowers are hummingbirds.

M. flemingii is similar to *M. puniceus* in corolla and coloration but the corolla lobes are smaller in size and the tube is strongly curved. This bird-pollinated species occurs on the Channel Islands.

The colonies of *Mimulus* are moderately to highly variable in several genetically determined characteristics of the shoot and flowers (Grant, 1963) and exhibit a geographical variation pattern. This variation is gradual and includes coloration, length of tube, corolla throat, corolla limb and pedicel lengths. From the hawkmoth flower to the bird flower, the colour shifts from yellow to red, the corolla shortens, and the pedicel length increases. The corolla tube is curved at the base and serves as nectar chamber in the bird-pollinated species *M. puniceus* and *M. flemingii*. All these species have the same chromosome numbers ($2n = 10$) (Wells, 1980) in contrast to other *Mimulus* species.

5.2 Evolutionary trends from red to non-red bird flowers

The corolla length of bird flowers is variable but generally does not exceed 10 mm. However, in some species this limit is greatly exceeded. Such a polymorphic corolla ranging from 15.4-37.8 mm is recorded in *Ipomopsis aggregata* and exhibits five different shades of coloration (Waser, 1983). According to the initial model, in this range of corolla length the floral coloration would be expected to be mostly red (cf. Fig. 20). As a matter of fact, Waser (1983) observed red floral colour in 12 out of 17 populations of this species. The remaining five populations had orange (2), purple (2), or pale red colours. Waser concluded that the flower colour in this species may vary geographically in a seemingly arbitrary way.

In comparing three *Castilleja* species of medium to small corolla size it is observed that they have a colour arrangement according to the gradient shown in Fig. 40.

The genus *Castilleja* (Scrophulariaceae) comprises 48 species (Grant, 1968) adapted to bird pollination in Western North America. The bracts, calyces, and corollas of these species are coloured and follow the patterns of red or non-red flowers, or the inflorescences exhibit a transitional stage between these two. Thus *C. miniata*, whose effective corolla length measures 15-16 mm, has red bracts; the flower belongs to the red group. *C. stenantha*, whose flowers are a little shorter, has red bracts and orange flowers 11-12 mm long, and demonstrates a transitional stage between a red and a non-red flower. *C. lemmonii* has very short-tubed, 10 mm long flowers, and bracts which are purple and yellow-green; it is a non-red flower (Fig. 40).

Transitional stages in colour and size may sometimes occur within a single species, e.g., *Fouquieria splendens*. The Fouquieriaceae are a small family restricted to arid portions of Mexico and adjacent Southwestern United States. The populations of the Sonoran and Chihuahuan Deserts exhibit a gradual west-east variation pattern involving reduction of corolla length. Populations with short or long orange-red corollas, extending from California to Coahuila and northern San Luis Potosí, are distinguished as *F. splendens* ssp. *splendens*. The subspecies *campanulata* is an allopatric population series in Durango with purple-pink or creamy-white corollas. An additional subspecies *breviflora*, with orange flowers, is found from San Luis Potosí to Hidalgo (Henrickson, 1972). All of these subspecies have the same chromosome numbers ($2n = 24$) (Henrickson, 1972).

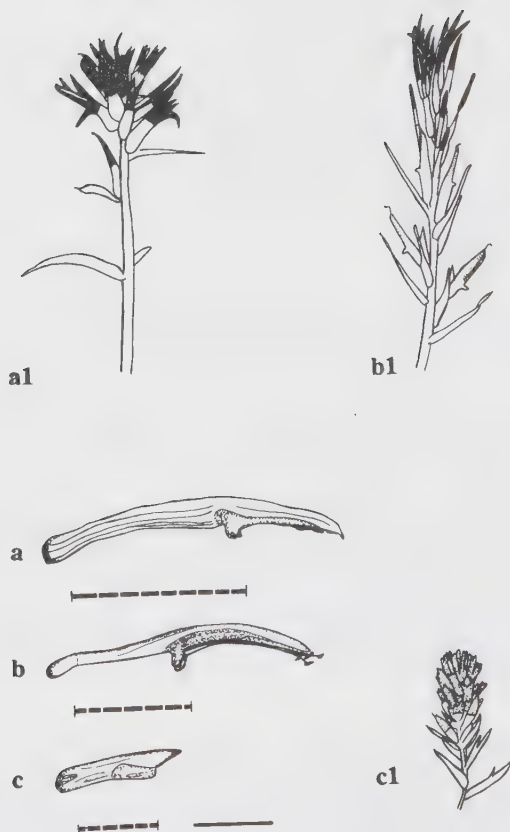


Fig. 40

Colour and corolla length features in three *Castilleja* species (Scrophulariaceae).

a-a1) *C. miniata*, b-b1) *C. stenantha*, c-c1) *C. lemmonii*. Comparison of the red, medium-sized corollas of *C. miniata* with the smaller-sized non-red flowers and red bracts of *C. stenantha* (orange), with the small non-red bracts and flowers of *C. lemmonii* (purple). a-c = corollas, a1-c1 = inflorescences; dotted lines indicate the effective corolla lengths, bar indicates 1cm.

The drawings are based on plant materials collected in the field.

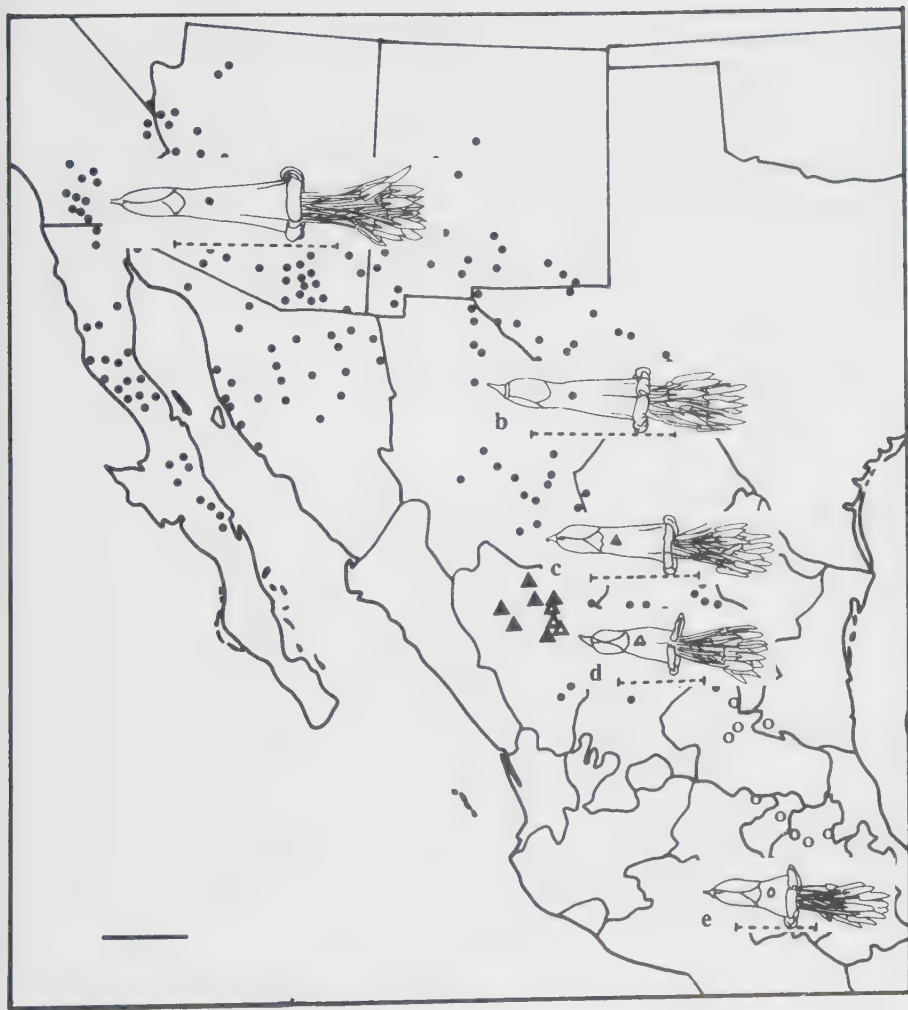


Fig. 41

Distribution, clinal size and colour variation in flowers of *Fouquieria splendens*. a-b) *F. splendens* (red). c) *F. splendens* ssp. *campanulata* var. *campanulata* (purple). d) *F. splendens* ssp. *campanulata* var. *albiflora* (white). e) *F. splendens* ssp. *breviflora* (orange). Bar indicates 1 cm, dotted lines indicate the effective corolla lengths.

Reproduced from Henrickson (1972), changed.

In this taxon a wide range in variation of floral and inflorescence size exists. This diversity, however, is by no means chaotic, but follows a pattern, with large structures in the far West gradually giving way to smaller structures in the eastern range (Henrickson, 1972). This west-east clinal variation pattern in flower colour and inflorescence conforms to the postulates of the initial model (Fig. 41). In the northern part of its distribution area, relatively long corollas (16-22 mm) are associated with orange-red flowers with yellow stamens, presenting the typical appearance of a red flower; in the southern part the corolla is shorter (8-10 mm) and non-red. *F. splendens* ssp. *splendens* is visited and pollinated by birds and by carpenter bees (Henrickson, 1972; Grant and Grant, 1968; Waser, 1979).

5.3 Discussion

The coevolution of flower morphology and bill morphology sets certain limits to the patterns of particular species (Feinsinger and Colwell, 1978). Flowers which are preformed in the manner of bird flowers by virtue of their floral structure possess an evolutive advantage over those in which several floral traits have to be modified.

Thus the sympetalous Dicotyledons, especially those of the family Scrophulariaceae, contribute most bird flowers in California (Grant & Grant, 1968). The bee-pollinated *Penstemon* species with their tubular corollas of suitable size were predisposed to bird pollination and account for 40 out of the approximately 300 species (Crosswhite and Crosswhite, 1981). Besides the genera *Castilleja* and *Mimulus* furnish over 53 taxa in bird flowers.

Other insect flowers were not preformed in the same way and have not yet fully attained the appearance of a bird flower. These flowers show transitional stages between an insect flower and a red bird flower. Grant and Grant (1968) list five genera in which some of the characteristics of hummingbird flowers are developed. These flowers are generally visited by both hummingbirds and some other classes of agents, usually bees (Lyon and Chadek, 1971; Straw, 1956; Spira 1980). In these flowers the coloration is mostly non-red, the corolla tube is either relatively short or relatively long, and they produce more nectar than their insect-pollinated relatives (Spira 1980). Anthecologically these species are functionally equivalent to non-red bird flowers of the small or large size categories.

Examples of flowers which are at the point of transition between two pollination syndromes (that have been recorded) are *Erythrina batolobium* in Mexico (Hernandez and Toledo, 1982) and *Scrophularia grandiflora* in the Canary Islands (Vogel et al., 1984).

Parapatric Gradient Speciation

Variation in the corolla size of bird flowers generally amounts to less than 10 mm. In populations of some species, however, this variation is exceedingly high and is often distributed gradually in space through populations. This clinal variation is well known in plant species, and is interpreted as an adaptation to the local environment. Examples are *Fouquieria splendens* and especially the *Mimulus calycinus* complex.

The gradual variation patterns of both the *M. calycinus* complex and the subspecies of

F. splendens do not coincide with appropriate gradual variations of bill and proboscis sizes of pollinators; it is rather a regional and general correspondence to pollinators of different size categories. The question is, why are the populations of such a complex interfertile?

According to Beeks (1962) and Mayr (1981) two or more parapatric populations would have become speciated in isolation, subsequently expanded their ranges, and finally hybridized in the zone of parapatric contact. However, this argument does not fully explain *gradual* variation.

Clark (1968) and Murray (1972) advanced an alternative theory according to which parapatric patterns are due to speciation by which the previously continuous range of ancestral species is disrupted along a step in an environmental gradient. Such gradual variants involve several morphological characters. This clinal variation when high imposes on the floral shape a shift-over from one pollination syndrome to another (e.g., from a red to a non-red bird flower in *F. splendens*). In a further step, reproductive isolation will prevent hybridization and establish the emerging species.

This applies to the *M. calycinus* complex and to *F. splendens* which both have high gradual variation patterns in coloration and lengths of corollas. The populations of both species complexes are connected by a reduced amount of interbreeding and gene flow, and polyploidy is not involved (Beeks, 1962; Henrickson, 1972). Moreover, these two species complexes are geographically associated with the species diversity in hummingbirds.

In the *Mimulus calycinus* complex in the North or North-West of the area of the *M. calycinus* complex, the insect-pollinated species dominate, in the South the bird-pollinated species.

In *F. splendens*, which comprises forms with both red and non-red bird flowers, the red populations predominate in the northernmost part of the area, which reflects the low hummingbird diversity of that region (all with medium bill length); the populations with flowers of non-red coloration are located in the southern part, where they provide nectar for small birds, reflecting a somewhat broader diversity in hummingbirds (Figs. 29 and 30).

Similar geographical correlations are recorded for the *Mimulus cardinalis* complex. This complex includes six species: *M. lewisii*, *M. eastwoodiae*, *M. cardinalis*, *M. verbenaceus*, *M. nelsonii*, and *M. rupestris*. All members of the complex have $n = 8$ chromo-

somes. The bee-pollinated *M. lewisii* is the most abundant and widespread species with the northernmost distribution of the complex. To the South, *M. cardinalis* and *M. verbenaceus* are adjacent bird flowers (Vickery, 1978).

M. cardinalis, however, exhibits transitional traits in floral morphology. The broad corolla throat and the yellow hairy ridges are typical bee flower traits, the red coloration and the reflexed lower corolla lobes are features of bird flowers. The remaining species (all bird flowers) occurring in Mexico have greater corolla lengths than has *M. cardinalis*.

The species diversity of hummingbirds within North America is geographically correlated with the species diversity of red-flowered *Penstemon* but negatively correlated with species diversity in non-red-flowered, insect-pollinated *Penstemon* (Crosswhite and Crosswhite, 1981).

Continuous variability in flowers of *Metrosideros collina* trees on the island of Hawaii has been observed by Carpenter (1976). Individuals above 900 m have brush-shaped and mostly red flowers pollinated by honeycreepers. Below 900 m yellow, partially fragrant flowers become abundant, traits which are associated with insect pollination.

Coevolution

Coevolution occurs when direct or indirect interaction of two or more evolving units produces an evolutionary response in each (Van Valen, 1982).

It is advantageous for an evolutionary unit to change its mean body size only if more energy for population expansion can be obtained at some other distribution of body size. In cases where body size is important in resource partitioning, such a change may usually have to await a decrease in the fitness of some other species, perhaps resulting in the local extinction of that species. Such parameters as the stability and predictability of energy sources can strongly affect its availability to a given species, and populations may be established in an environment of lower available energy, but an evolutionary response occurs almost solely when more energy for species expansion is obtained as a result of the evolution (Van Valen, 1982). If solar radiation causes climatic warming, then both plants and birds are likely to evolve into potential niches, at least in temperate latitudes.

The hummingbirds will respond by gradually changing their variance in body size, and when the limits of their range of variation have been reached, reproductive isolation will facilitate the speciation process. Analogous gradient evolution in the floral traits will

involve corolla length and coloration of flower simultaneously, according to the patterns described above.

A similar gradual shift from one syndrome of pollination to another is reported in *Ipomopsis aggregata* (Paige & Whitham, 1985), although the gradient is not spatial but temporal. In some populations or individuals of this species, plants shift from bird flowers to hawkmoth flowers during the flowering season by altering their floral colour, time of nectar secretion, and scent (Paige, pers. comm.). This confirms that certain plants possess a high degree of evolutionary potential for altering their floral shape.

Plant and pollinator coevolution is not the result of simple allelic change such as differences in floral colour which in turn can influence the likelihood of being visited by the local pollinators as proposed by Waser (1981). Coevolution is of a more non-specific and indirect nature (Gilbert, 1979), rather involving gradients in the whole assemblage of floral traits and the traits of pollinators which simultaneously undergo coordinated alterations in a spatial or temporal mode.

This is just about what is observed in the plant-pollinator communities in which evolution of the important traits such as floral colour and the shapes and dimensions of flower and pollinator bill follow definite pathways in a statistical sense.

Conclusion

An array of bird flowers and pollinators in Western North America just now seem to be undergoing a process of speciation which is being promoted by environmental factors, above all, climatic factors.

The evolutive trends go from insect flowers to red bird flowers, and from red bird flowers or insect flowers to non-red bird flowers. The birds start with medium bill sizes which variation will alter toward longer and shorter sizes.

Speciation of bird-pollinated plants and pollinators in western North America is hypothesised to be the result of mainly parapatric gradient speciation in plant-pollinator communities.

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6. SUMMARY

The present thesis examines the syndrome of ornithophily: the pollination of flowers by birds, especially regularities in the colour and shape of flowers, the bill shape of pollinators, and their correlation and evolution.

For visualizing floral colours in the bird visual system a photographic method was worked out. Pictures so obtained indicate an ability of hummingbirds to see UV guides on yellow insect flowers. The reflectance of 38 Californian bird-pollinated plants is weak in the near UV (310-395 nm). Thus, contrary to what is the case in bee flowers, possible nectar-guides on bird flowers are situated within the human visual range.

Over 1100 taxa of bird-pollinated plants and 560 bill lengths of their main bird pollinators (Trochilidae, Nectariniidae, Drepanididae) all over the world were investigated (field work in California and Hawaii, and data from literature). Thus, the syndrome of ornithophily turns out to contain both red and non-red bird flower groups, which contrast in size as well as in colours.

Red flowers are frequent and not always possess nectar-guides which are mainly yellow, white, violet, or black, all good contrasting colours on red flowers. These species have flower tubes of medium length and are pollinated by generalists with medium bill lengths.

Non-red flowers mostly have orange, purple, blue, yellow-green, white, and black corolla and nectar-guide colours. Non-red flowers have either long or short tubes. These flowers are rare and are pollinated by birds with suitable bill lengths.

It is shown that the plant-pollinator communities are organized according to the above-mentioned principle on a world-wide scale with the exception of that of Australian bird flowers which lack the long tube category.

The distribution of birds and flowers is geographically correlated. Variation in bill size of hummingbirds and nectarivorous birds is highest in the tropics and declines towards temperate latitudes. The corolla length of bird flowers shows parallel characteristics.

It is suggested that bird flowers of western North America evolved and evolve by a *gradual* speciation process from insect flowers. A number of plant species have flowers in a transitional stage between insect flowers and red bird flowers. In terms of flower function

these species can be compared to non-red bird flowers of the small or large size categories, respectively.

6.1 ZUSAMMENFASSUNG

In der vorliegenden Arbeit wird einigen Aspekten der Ornithophilie (Bestäubung der Blüten durch Vögel) nachgegangen, wie Farbe und Form der Blüten sowie die Schnabelformen und -längen der Bestäuber; es werden Beziehungen dieser Strukturen zueinander gesucht, sowie ihre mögliche Evolution diskutiert.

Mittels der Methode der Falschfarbenfotografie wird eine Transformierung von Blütenfarben in den Sehbereich der Vögel (Kolibri) erreicht. Anhand solcher Bilder kann gezeigt werden, dass Kolibris UV-Saftmale auf gelben Blüten sehen können. Hingegen zeigen 38 Blüten von auf UV-Musterung hin untersuchten kalifornischen Pflanzen nur unwesentliche Reflexionen im nahen UV (310-395 nm). Es wird gefolgert, dass im Gegensatz zu Bienenblumen mögliche Saftmale der Vogelblumen nicht im UV-Bereich zu finden sind, sondern in dem für den Menschen sichtbaren Bereich des Spektrums.

Ueber 1100 Taxa vogelbestäubter Pflanzen und 560 Schnabellängen der wichtigsten Blumenbestäuber (Trochilidae, Nectariniidae, Drepanididae) wurden gemessen, oder die Daten aus der Literatur zusammengetragen und ausgewertet.

Es ergab sich als Befund, dass zum Syndrom der Ornithophilie zwei, einander in Farbe und Korollenlänge, kontrastierende Gruppen von Vogelblumen zu zählen sind: rote und nicht-rote Vogelblumen.

Die roten Vogelblumen sind häufig anzutreffen und besitzen Saftmale, die vor allem gelb, weiss, violett, oder schwarz gefärbt sind, alles Farben, die mit dem Rot der Blüte gut kontrastieren. Die roten Blumen haben im allgemeinen mittlere Korollenlängen und werden von den Generalisten unter den Bestäubern angefliegen, die mittlere Schnabellängen aufweisen.

Nicht-rote Vogelblumen sind seltener, haben hauptsächlich orangene, purpurne, blaue, gelbgrüne, weisse oder schwarze Blüten und Saftmale, wobei die Kronenröhre entweder lang oder kurz ist.

Es konnte gezeigt werden, dass die Pflanzen-Bestäuber-Gemeinschaften stets nach oben genanntem Prinzip organisiert sind, und dies auf weltweiter Ebene, wobei australische Vogelblumen eine Ausnahme machen, indem dort keine langröhrigen Vogelblumen ausgebildet worden sind.

Die Verteilung von Vögeln und Blüten ist geographisch korreliert. Die Variationsbreite

von Schnabellängen und Korollenlängen aller Arten insgesamt ist in den Tropen am grössten und verringert sich allmählich zu den gemässigten Zonen hin.

Es wird vermutet, dass die ornithophilen Blüten im westlichen Nordamerika durch einen *graduellen* Artbildungsprozess evoluiert sind und noch evoluieren, nämlich über Insektenblumen via Uebergangsblumen zu Vogelblumen. Funktionell zeigen diese Uebergangsblumen Parallelen zu den nicht-roten Vogelblumen.

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